

STUDIES ON POPULATION REGULATION OF TWO
ANNUAL WEEDS, *GALINSOGA CILIATA* (RAF.)
BLAKE AND *G. PARVIFLORA* CAV.

By

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THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF
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I certify that the thesis entitled "Studies on population regulation of two annual weeds, Galinsoga ciliata (Raf.) Blake and G. parviflora Cav." submitted by Mr. Jai Prakash Narain Rai, M.Sc., for the Degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. Degree. This work has not been submitted for any Degree of any other University.

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General Introduction

GENERAL INTRODUCTION

How succeeding generations of a plant species persist in natural populations in almost same number in spite of its enormous offspring production, pricked to Darwin as far back as 1859, who questioned, "Look at a plant in the midst of its range, why does it not double or quadruple its number?" In fact a species population has innate potential to increase in size geometrically as a result of 'the passion between the sexes' (Malthus, 1793). But this potential is never realized in nature, and often the population of a species tends to remain constant showing fluctuations around mean value. This indicates that certain limitations are imposed by the environment, which either reduce the birth rate or enhance the death rate. The environmental factors that usually control the population growth and structure irrespective of density are the available resources, climatic conditions, population interaction, disease etc. Besides, the density-induced regulation of population size also occurs. Although attempts have been made to understand and quantify the effect of density-dependent and density-independent factors on the population growth of plant species (Sukatchev, 1928; Tadaki & Shedei, 1959; Yoda et al., 1963; White & Harper, 1970; Myerscough & Marshall, 1973; Tripathi & Gupta, 1980; Clay & Shaw, 1981; Tripathi & Yadav, 1982), the exact mechanism of population regulation is yet to be fully understood. In fact, under Indian conditions not much work has been done on the ecology of populations as a whole. In view of

this Tripathi & Dwivedi (1978) have stressed the need for studying the population ecology of plants of different growth habits under varied environmental conditions.

Studies on the dynamics and regulation of populations in nature inevitably involve demographic analysis at regular time intervals. The demographic analysis of many plant species has been done by Professor J.L. Harper and his coworkers (Harper & White, 1971; Sarukhan & Harper, 1973; Hawthorn & Cavers, 1976; Mack, 1976; Watkinson & Harper, 1978) while the behaviour of plant populations in pure and mixed stands has been studied by De Wit and his group and many other workers (e.g. De Wit, 1961; De Wit et al., 1966; Tripathi & Harper, 1973; Bazzaz & Harper, 1976; Mack & Harper, 1977; Berendse, 1979, 1981). The survivorship and dynamics of several perennial grass and herb populations from different geographic regions have been studied by a number of workers (e.g. Williams, 1970; Antonovics, 1972; Sarukhan & Harper, 1973; Hawthorn & Cavers, 1976; Johnson & Thomas, 1978; Bishop et al., 1978; Kushwaha et al., 1981; Law, 1981; Yadav & Tripathi, 1981; Silvertown & Dickie, 1981; Schellner et al., 1982) and of biennials by Holt (1972) and Klemow & Raynal (1981). Although the annuals pose relatively lesser practical problems (Harper & White, 1974), the population studies of annual plant species have engaged the attention of very few workers. Mack (1976) studied the survivorship of Cerastium atrovirens and Sharitz & Mc Cormick (1973) studied the population dynamics of two

competing non-weedy annuals and proposed the hypothesis that the population regulation in these species is mainly through interspecific competition for soil moisture. The seed population dynamics of winter annual grass Vulpia fasciculata has been studied by Watkinson (1978) and natural regulation of populations of the same has been described by Watkinson & Harper (1978), who emphasized the role of density in regulation of populations. Recently Weiss (1981) studied the population dynamics of Emex australis and reported heavy mortality during seedling stage especially in dense populations. The density increase may also reduce the reproductive potential of the species populations as reported by several workers (Palmlblad, 1968a; Tripathi, 1968; Myerscough & Marshall, 1973; Williams & Ingber, 1977; Tripathi & Gupta, 1980; Clay & Shaw, 1981; Trivedi & Tripathi, 1982a; Rai & Tripathi, 1982a).

Besides self crowding, the growth of associated vegetation also regulates the population size either through resource competition (Harper & Gajic, 1961; Sagar, 1970; Putwain & Harper, 1970; Mack & Harper, 1977; Dwivedi & Tripathi, 1980; Yadav & Tripathi, 1981) or through production of some toxic substances which inhibit the seed germination and growth of neighbouring plant species (Muller, 1969; Rice, 1974; 1979; Friedman et al., 1977; Hussain & Godoon, 1981; Rai & Tripathi, 1982b). The allelochemicals produced from plants have also been reported to regulate the rhizospheric microbial population (Singh, 1977; Tripathi et al., 1981).

Kulman (1971) laid emphasis on the role of herbivory in population regulation and reported that predation results into increased mortality and reduced seed and biomass production. Werner (1977) studied the effect of predation by Lepidopteron larvae on regulation of teasel population whereas Bentley & Whittaker (1979) emphasized the role of grazing by Chrysomelid beetle in the distribution of Rumex spp. in nature.

In the present investigation two annual weeds Galinsoga ciliata (Raf.) Blake and G. parviflora Cav. were selected for studying their detailed demographic analysis with a view to identify the factors involved and their relative importance in the regulation of the population of these weeds. The two species of Galinsoga grow abundantly in croplands and wastelands of Meghalaya. They are closely related sympatric pair of species with synchronous life cycle. These characters make these species ecologically interesting. Moreover, population ecology of these weeds has not been studied at all.

The studies on population regulation of these two weeds have been made to cover the following aspects:

- i) The demographic analysis of seedling cohorts of the weed populations with respect to recruitment, mortality and reproduction at cropland and wasteland habitats.
- ii) The effect of associated plant species and established mature plants of the two weeds on regulation of their seedling populations.

iii) Allelopathic effect of Eupatorium riparium Regel on population regulation of these two weeds.

iv) The effect of factors such as seed sowing density, sowing pattern, population density, soil texture and soil moisture and nitrogen level on the population regulation of weeds.

v) The effect of herbivore predation on competitive ability and growth of the two species.

vi) The effect of light intensity and 2,4-D on the weed populations.

The experimental data on various aspects mentioned above have been presented in chapters III to VIII which follow 'General Introduction', 'Review of Literature' (Chapter I) and 'Description of Study Site and Selected Species' (Chapter II). The 'General Introduction' outlines the objectives of the thesis while the 'Review of Literature' covers the published literature to show the present status of the subject. Chapter II deals with the soil, vegetation and climate of study site. It also includes the distribution and description of the two species. Though each chapter is provided with a separate discussion of results, the major findings of the whole thesis have been discussed under 'General Discussion' in an integrated manner. To avoid repetition, some important references that have been included in 'General Introduction' have been omitted from the 'Review of Literature'.

The studies on dynamics and regulation of population may prove quite useful in devising effective weed control

measures, as these studies may reveal the ecological conditions that may influence the natality, mortality, survivorship and ultimately population growth of these weeds. On the basis of data collected on various population parameters, working population model can be synthesized through which the reaction of a particular environmental factor on the population behaviour of the weed can be predicted. Thus, although the present study is largely of fundamental nature, it has applied value too.

CHAPTER I

Review of Literature

REVIEW OF LITERATURE

Despite innate potential to increase their numbers in geometric progression, the organisms do not exhibit unlimited population growth. The causes of this are still obscure, although understanding the mechanism of population size regulation is of vital importance to both pure and applied ecologists. Solomon (1964) opined that the population regulation is generally brought about both by density-dependent and density-independent processes while Tripathi & Dwivedi (1978) emphasized the need for identifying various factors controlling the population growth and for studying the relative importance of each of these factors and their interacting influence on plant populations in nature. Such studies are possible only when the demographic analysis of individuals right from the early seedling stage till the senescence is made. The demographic studies of plant population made by various workers covering a wide range of species have been reviewed by Harper & White (1974). The present review is, therefore, mostly devoted to those papers related to the subject that have appeared after the publication of the review of Harper & White (1974).

Callaghan (1976) pointed out that the growth reproduction and death of individuals in plant population are affected by the environmental factors (both biotic and abiotic) within the genetic limit of the populations. The effect of other organisms including the individuals of same species, via grazing, predation, competition for limited resources and

allelopathy, is a potent factor of population regulation. The natural calamities like sudden change in temperature, heavy precipitation, frost, storms and long spell of dry weather also cause wide spread destruction to the populations. The death caused by such physical factors has been called as 'catastrophic death' by Warren Wilson (1967). Besides these, the manipulation of populations by human activities is also of great significance in regulation of population size (Harper, 1960).

There are two main ways in which the response of plants to environmental factors may regulate population size:

- i) mortality influencing the number of survivors and
- ii) plasticity causing reduction in size and reproductive capacity of individuals.

Population regulation through mortal response :

In plants, the recruitment of new individuals takes place through the germination of seeds or sprouting of vegetative propagules, which after growth and maturation produce large number of seeds. Despite enormous seed production, many plant species maintain their population size at a given level over the years, which indicates that quite a large number of seeds fail to produce seed bearing plants. Sagar (1970) found only one out of 17,100 seeds of Papaver rhoeas and 1,000 seeds of Senecio vulgaris succeeds in producing a seed bearing plant. Similarly, Yadav & Tripathi (1981) also found that out of 4,625 seeds of Eupatorium odoratum only one could produce a fertile

plant. This implies that heavy mortality of individuals must be taking place at various stages of the life cycle. The seeds die and degenerate, the seedlings die and the established adult plants also die.

The seed population in the soil, which regulates the regeneration of vegetation (Thompson & Grime, 1979) is influenced by the two processes i.e. seed input to the soil and seed loss from the soil. The seed input to the soil seed pool depends upon the seed production by the growing plant populations every year and on the environmental factors which affect the number of seeds reaching the soil seed bank. A large fraction of total seeds produced by the vegetation is carried away by wind and water to distant places. For example, Yadav & Tripathi (1981) observed that more than 87% of the total seed population of Eupatorium odoratum was lost to wind and water. Predation and grazing also affect the number of seeds entering the seed pool (Sarukhan, 1974; Keeley & Hays, 1976; Keeley, 1977).

Although among all plant parts the seed is least susceptible to the rigours of climate and other unfavourable conditions, a very large fraction of soil seed population fails to produce seedlings. Sagar (1959) found only 11% of surface sown seeds of Plantago lanceolata and less than 3% of the seeds of P. major as seedling after one year period. A similar observation was made by Jefferies et al. (1981) with salt marsh annual Salicornia europaea which indicates the death of large fraction of the soil seed population. The causes of death of

such enormous population of seeds are numerous. A fraction of seed population may lose viability and degenerate due to unfavourable environmental conditions like fluctuating temperature and high humidity. A large number of weedy species studied by Roberts (1979) and Roberts & Feast (1972) showed that the seeds lose viability rapidly and the seeds of only a few species could survive for more than five years. Further, a good percentage of seeds is also induced or enforced into dormancy (Sarukhan, 1974; Baskin & Baskin, 1975; Gorski et al., 1977; Mukherjee et al., 1980). Besides, the soil microorganisms and pests also cause mortality of the seeds in soil (Foster, 1964; Sarukhan, 1974) resulting into reduction in population size.

Under favourable conditions a fraction of the soil seed population germinates to give rise to seedlings which are exposed to varied influences of different environmental factors. The newly born seedlings are usually considered to represent the most delicate phase of plants' life. A lot of work has been done showing heavy juvenile mortality in seedling populations of several plant species (Williams, 1970; Hett, 1971; Sarukhan & Harper, 1973; Sharitz & Mc Cormick, 1973; Hett & Loucks, 1976; Bazzaz & Harper, 1976; Mack, 1976; Yadav & Tripathi, 1981; Silvertown & Dickie, 1981; Weiss, 1981; Law, 1981). Sharitz & Mc Cormick (1973) argued that heavy mortality during seedling establishment is common in colonizing species which produce large number of seeds. Mack (1976) and Watkinson & Harper (1978) have also emphasized the occurrence of Type II and III

survivorship curve (Deevey, 1947) in species capable of producing large number of seeds in contrast to those which produce lesser number of seeds and exhibit Type I survivorship curve. These studies indicate that the heavy mortality of seedlings in such species which produce large number of seeds is a prerequisite for an effective regulation of population size.

The established plants which predominantly respond through plasticity to various environmental stresses also show constant mortality throughout their life and hence exhibit Type II survivorship curve (Tamm, 1956; Rabotnov, 1958; Sagar, 1959; Foster, 1964; Antonovics, 1972; Bishop et al., 1978). The studies made by various workers (Langer, 1956; Robson, 1968; Sarukhan & Harper, 1973; Hawthorn & Cavers, 1976; Yadav & Tripathi, 1981) on several plant species revealed that the plant mortality is maximum in the active growing season of population. Further, the mortality has been reported to be greater in monocultures than in polycultures (Tripathi & Harper, 1973; Bach & Hruska, 1981). The greater mortality which often occurs during period of most rapid growth might be construed as evidence for density effects, as the effect of competition for resources are likely to be most severe during active growth phase.

The density-dependent mortality is known in Agrostemma githago (Harper & Gajic, 1961), Papaver spp. (Harper & Mc Naughton, 1962), Spergula vernalis (Symonides, 1974), Mirabilis hirsuta (Platt, 1976). Bromus spp. (Wu & Jain, 1979) and Poa annua (Law, 1981) but this is by no means general

(Sarukhan & Harper, 1973; Watkinson & Harper, 1978; Klemow & Raynal, 1981). This indicates that density effect is species-specific. But the studies of Pemadasa & Lovell (1974) on four dune annuals and of Keddy (1980) on Cakile edentula revealed that the density-dependent mortal response might be changed by soil condition and exposure treatments. Keddy (1981) further argued that unlike density-dependent mortality, density-independent mortality rate remains constant.

Antonovics (1972) pointed out that the causes of death rates are influenced by the environmental and genetic factors and emphasized the importance of the population decay rates in the genetic adjustment in a varying and unpredictable environments. On the basis of his observations on Anthoxanthum odoratum he argued that during seedling establishment there may be selection of characters which show differential rates of mortality in different phases of the life span of individuals. For example, Williams (1970) reported Type III survivorship curve in case of Danthonia caespitosa with heaviest mortality during young stage in contrast to the observation of Canfield (1957) on three perennial grasses, who found Type I survivorship curve (i.e. lesser risk of death in young and middle period of age and high mortality risk in old age), while Johnson & Thomas (1978) demonstrated that survival of Hieracium piloselloides followed Type II survivorship curve. However, these studies also support the logic that plant mortality is a prerequisite to population regulation of a species, whether it is occurring at seedling stage or at later stage.

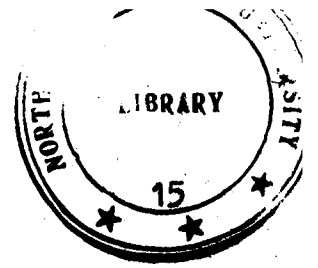
Population regulation through plastic response :

In contrast to mortality at high density, plants generally respond to moderate density through plastic reduction in size and reproductive capacity (Antonovics & Levin, 1980). The effect of plant density on populations has been studied by many workers (Sukatchev, 1928; Tadaki & Shedei, 1959; Harper & Gajic, 1961; Harper & Mc Naughton, 1962; Raynal & Bazzaz, 1975a; Khan & Bradshaw, 1976; Tripathi & Yadav, 1982). Yoda et al. (1963) established a relationship between the mean dry weight per plant and the density of surviving individuals in pure populations of several herbaceous plant species and propounded the well known $-3/2$ thinning law, which was later on confirmed by White & Harper (1970) in mixture of two similar plant species and by Kays & Harper (1974) in grass sward. Bazzaz & Harper (1976) tested the thinning law in mixture of two very different species viz., Lepidium sativum and Sinapsis alba. Based on the consideration of a given species grown within mixed stand, Kays & Harper (1974) and Bazzaz & Harper (1976) suggested that the thinning law is not applicable to such cases and, therefore, cannot be used as supporting evidence for density effects in complex communities. A similar report has been made by Malmberg & Smith (1982) in mixed populations of Medicago sativa and Trifolium pratense. Hutchings (1979) assessed the validity of the $-3/2$ power law in nine clonal perennial herbs, and suggested that genets follow the power law in contrast to ramet populations which are not necessarily thinned in direct response of their growth. Recently, Westoby & Howell (1981) found a change

in thinning line from $-\frac{1}{2}$ to zero in populations of Beta vulgaris growing under different light conditions.

The effect of population density has also been studied on plant to plant variation in yield. Stern (1965) reported that plant weight distribution in Trifolium subterraneum was closer to the log normal at low density compared to skewed distribution at high density. Obeid et al. (1967) found essentially similar behaviour in studies of inter-plant variation in fiber flax (Linum usitatissimum) population. Koyama & Kira (1956) argued that the log normal distribution is the outcome of the exponential nature of fundamental growth process while skewed distribution or L-shaped frequency curve is resultant of competition which increased the variability of the relative growth rate of individuals in population.

The reduction in plant weight in response to density affects the reproductive potential (Harper & White, 1974) through reduction in several components of fecundity (i.e. number of flowering plants in a population, number of flowers per plant and number of seeds per fruit). For example, the decreased fertility in plant populations with increasing density has been reported by Harper & Gajic (1961), Marshall & Jain (1969), Myerscough & Marshall (1973), Thomas & Dale (1975), Tripathi & Gupta (1980), Tripathi & Yadav (1982) and Rai & Tripathi (1982a), and the reduction in per plant capitula or propagules by Putwain et al. (1968), Palmblad (1968a), Tripathi



(1968), Williams & Ingber (1977), Watkinson & Harper (1978), Weiss (1978), Tripathi & Gupta (1980), Barkham (1980), Law (1981), Clay & Shaw (1981), Tripathi & Yadav (1982) and Waite & Hutchings (1982). The change in number of seeds per fruit, although uncommon, has been observed by Palmblad (1968a) and Myerscough & Marshall (1973) in response to density stress. These studies highlight the gradual and stage-wise reduction in seed production which ultimately regulates the size of population.

Although the reproductive characters (fecundity) have been reported to respond to density, the relation between the response of the characters and density is variable (Obeid et al., 1967; Krebs, 1971; Harper, 1977). However, Primack (1978), based on his observation on seed production by Plantago coronopus, concluded that all the components of fecundity are equally important in regulating the seed production in stressed environment.

Like frequency distribution of biomass, Clay & Shaw (1981) reported a skewness in frequency distribution of flowers per plant with increasing density of Diamorpha smallii in natural conditions. The trend of increased skewness with density reported by them is in agreement with the observation of Obeid et al. (1967) on Linum usitatissimum grown at three density levels, who reported relatively greater skewness of capsule as compared to that of biomass. This is primarily due to non-linear relationship between plant weight and reproduction.

Holliday (1960) and Donald (1963) have shown that, whereas individual plant weight may exactly compensate for increasing density (to give constant final yield) reproductive output may over compensate the density increase i.e. the ratio of reproductive to total yield may fall at high densities.

Snell & Burch (1975) observed 3-fold reduction in reproductive effort of Chamaecyse hirta due to density stress. In Cyperus rotundus, under low density conditions ~~the~~ dry weight was partitioned into tubers. However, under high density conditions more dry weight was partitioned into tubers rather than inflorescences (Williams et al., 1977). Haller & Abrahamson (1977) observed in Fragaria virginiana that increased competition among high density grown plants resulted in lower total biomass when compared to low density grown plants while the allocation to biomass in reproductive organs (both seed and vegetative) was higher in low density grown plants. Similar observation has been made by Waite & Hutchings (1982) with Plantago coronopus, where 3-fold increase in density resulted into reduction in reproductive allocation from 47% to 31%. These studies depict the density-dependent regulation of population size.

Harper, (1961, 1967), on the basis of his work on Bromus rigidus and B. madritensis generalized that plant species adjust seed number in response to density stress in such a manner that seed number per unit area is constant over a wide range of densities. Palmblad (1968b) observed that the seed production

per individual of Senecio sylvaticus and S. viscosus increased with the decrease in severity of competition. In contrast to this, the reproductive allocation in certain plant species has been observed to increase with increasing harsh conditions (Gadgil & Solbrig, 1972; Whigham, 1974; Hickman, 1975). According to Hickman (1975) seed output per unit area does not remain constant over a wide range of densities, and that average plant weight and seed output per plant can be predicted from plant density. Conversely, there are reports indicating that the allocation of resources to reproductive structures remains unaffected by density stress (Harper & Ogden, 1970; Ogden, 1974; Bradbury & Holstra, 1976; Abrahamson & Hershey, 1977; Raynal, 1979; Thompson & Beattie, 1981; Tripathi & Yadav, 1982).

Such erratic effects of population density on various plant species may be explained on the basis of "ecological effective distance" (Antonovics & Levin, 1980), which defines the limiting or threshold distance at which neighbour effect ceases. Clay & Shaw (1981), based on the calculation of ecological effective distance for several species under a variety of environment suggested that it should not be considered fixed; these values will rather vary from one species to another depending on environmental fluctuations and the stage of life cycle. This also provides a clue for understanding the modifying influence of nutrient status of the soil on density-dependent response of Papaver spp. (Harper & Mc Naughton, 1962), dune

annuals (Pemadasa & Lovell, 1974), Eupatorium spp. (Tripathi & Yadav, 1982) and Plantago major (Trivedi & Tripathi, 1982a).

In contrast to the attention given to the importance of density-dependent factors in determining the fate of established plants, the studies pertaining to the effect of seed density upon germination are few and far between. Ballard (1958) and Palmblad (1968a) reported both positive and negative response to sowing density among certain weedy species. Based on his own tests of 11 species and of 11 other species reported in the literature, Linhart (1976) argued that positive density-dependent responses appear to be characteristics of species of closed habitats while neutral or negative responses occurred in weedy species of open habitats. Waite & Hutchings (1978) reported that germination and salinity tolerance of Plantago coronopus seeds are enhanced when seeds were sown in clumps. The extent of the positive density-dependent response, and the optimum clump size for maximum germination were found to be dependent on salinity level and nature of substrate. Linhart (1976) suggested that the positive germination response to clumping of seeds may be either due to physiological factors (possibly through production of certain chemicals) and/or due to combined force of several simultaneously growing radicles that may help them emerge.

Working with dune annuals, Symonides (1978) found a neutral response of seed germination to density while Inouye (1980) found a strong negative response to density of seeds in

desert annuals of Arizona. Recently, Rai & Tripathi (1982a) have also reported a negative response to density of seeds in two species of Galinsoga, which indicates as to how the seed sowing density exert itself as a feed back mechanism of population regulation.

Population regulation through density-independent process :

Besides 'density-dependent' regulation, the populations are also regulated in a big way by physical factors of environment particularly at seedling emergence and seedling establishment stages. This may be explained applying the concept of 'safe site' (i.e. locations ideal for germination and establishment) as developed by Harper et al. (1965). Thus, the number of such sites may have strong regulatory effect on the size of seedling population and this effect will be more and more severe with increase in density of seeds and seedlings, as the number of sites is not infinite. Initially with an increase in number of seeds in a habitat, the chances of a seed finding a safe-site is increased but later when all the sites are exhausted any further increase in density may not contribute at all to the seedling population until more sites are made available.

The physical factors which create a variety of microsites are soil fertility, soil texture, soil moisture and light intensity. The plant populations also respond to these factors through mortality and plasticity. Sukatchev (1928) in Matricaria inodora, Andel & Rozema (1974) in Chamaenerion angustifolium and

Nobel et al. (1979) in Carex arenaria found increased mortality at fertilized soil, in contrast to the observation of Myerscough & Marshall (1973) on Arabidopsis thaliana and of Trivedi and Tripathi (1982a) on Spergula arvensis and Plantago major. Similarly, the plastic increase in reproductive allocation at high fertility level has been observed by Snell & Burch (1975) in Chamaecypar hirta and by Tripathi & Yadav (1982) in Eupatorium spp., while in Senecio vulgaris (Harper & Ogden, 1970) and in S. sylvaticus (Andel & Vera, 1977) reproductive allocation has been reported to be independent of nutrient status.

In drought habitats, Tazaki (1960), Peterken (1966), Cavers & Harper (1967), Friedman & Orshan (1975), Seif El-Din & Obeid (1971), Miles (1972) and Ungar et al. (1979) found a heavy seedling mortality in various plant species, which signifies the importance of soil moisture in population regulation. Trivedi & Tripathi (1982b) also reported a drastic reduction in seed output by Spergula arvensis in moisture stressed conditions. They observed better growth of this weed in sandy soil than in clay-rich soil. Watkinson (1982) observed that drought during flowering phase of Vulpia fasciculata reduced seed setting and resulted into a marked density-dependent reduction in fecundity. Working on the relationship between distribution of three legume species and environmental factors, Foulds (1978) reported that soil moisture is a limiting factor in distribution of Trifolium repens in the grasslands of the U.K., Cook (1965) studied the role of edaphic factors and competition in

the regulation of population of Eschscholzia californica. Palmblad (1968a) observed the effect of seed sowing density, soil surface; fertilizer and moisture on the population behaviour of many weedy species in field and glasshouse conditions. He suggested that the self-controlled germination, mortality and plasticity may contribute to the population regulation of weedy species which produce more seeds per unit area than required for their maintenance. Sharitz & Mc Cormick (1973) studied the population dynamics of Sedum smallii and Minuartia uniflora in field and controlled conditions of Georgia and proposed the hypothesis that the population regulation of these species is mainly through interspecific competition for soil moisture. They further observed that abiotic factors tended to cause reduction in growth of the individuals while interspecific competition favoured mortality of the individuals.

Patterson (1980) studied the partitioning of plant biomass in Cogon-grass (Imperata cylindrica) from shaded and exposed habitats and found that the allocation to reproductive activities was lesser under shaded conditions. A similar observation was made by Gulmon & Chu (1981) with the Chaparral shrub, Diplocais surantiacus. These studies highlight the role of light in population regulation.

The lower temperature of environment has also been considered to be effective in population regulation. For example, Symonides (1974) found a mortality peak in pure population of Spargula vernalis in dunes of Poland due to frost. Yadav

& Tripathi (1981) reported a severe mortality during winter for both seedlings as well as adult populations of Eupatorium odoratum.) While working on population dynamics of Erigeron canadensis - a successional winter annual in Illinois, Regehr & Bazzaz (1979) reported 16 to 86% plant mortality due to frost heaving. Recently, Pearson & Shah (1981) observed a significant reduction in seed production by Paspalum dilatatum grown under low temperature condition.

Effect of associated plant species: The associated vegetation and established plant population exercise great regulatory influence on the population of newly recruited individuals either through resource competition and/or through production of some toxic substances (allelochemicals). Tripathi & Dwivedi (1978) suggested that the fundamental niche of a species may be restricted to a smaller hyper volume due to interference caused by the presence of associated species. Relatively poor seedling establishment in established communities (Tamm, 1956; Cavers & Harper, 1967; Putwain & Harper, 1970; Singh, 1980) also confirms the above statement. Sagar & Harper (1961) and Dwivedi & Tripathi (1980) found that among the associated species, grasses exercise greater regulatory influence as compared to dicots. Sagar (1970) reported a better vegetative and reproductive growth of Plantago lanceolata when the associated vegetation was removed. Similarly, Raynal & Bazzaz (1975b) found an increased seed output by three summer annuals in plots from where the winter annuals were removed. Cronin (1976) reported that after removal of tall larkspur (Delphinium

barbeyi) the forb dominated communities were converted into grass dominated communities.

While studying the competitive effect of Zygophyllum dumosum plants on seedlings of Artemisia herba-alba, Friedman (1971) reported that the seedling growth was considerably suppressed and the suppression became severe as the distance between mature plant and seedlings decreased. A similar conclusion has been drawn by Mack & Harper (1977) and Yadav & Tripathi (1982) in other plant species. Gupta & Tripathi (1979) reported that when Bothriochloa pertusa was introduced to already established population of Dichanthium annulatum, it showed substantial reduction in yield and complete suppression in reproductive growth. Yadav & Tripathi (1981) also reported that when E. odoratum seedlings were either grown with its own adult plants or with other associated species, it showed poor vegetative and reproductive growth. Andel & Rozema (1974) also observed suppressed growth of seedlings of Chamaenerion angustifolium grown with the associated species and attributed the growth suppression to a keen competition for water between associated vegetation and seedling population where the former happens to utilize the available resources more effectively.

Relatively greater survival and better growth of early emerging cohorts of Ranunculus spp. (Sarukhan & Harper, 1973), Plantago spp. (Hawthorn & Cavers, 1976), Rumex spp. (Weiss & Cavers, 1979) and Emex australis (Weiss, 1981) than the late emerging ones might be construed as evidence for the effects of

established plant species in population regulation. Ross & Harper (1972) suggested that the late emerging individual has to face relatively severe competition to occupy biological space as compared to that emerged earlier. Ford (1975) and Harper (1977) have also emphasized the significance of emergence time in seedling fitness.

Besides resource competition from associated species, the production of some allelochemicals also regulates the size of neighbouring plant species (Rovira, 1969; Whittaker & Feeny, 1971). Many studies reviewed by Rice (1974, 1979) reveal that allelopathy is a potent factor in determining the pattern and process of vegetation. Working on the grassland vegetation of California, Bell & Muller (1973), Hull & Muller (1977) and Parker & Muller (1979) respectively reported the dominance of Brassica nigra, Stipa pulchra and Pholistoma autitum over other plant species through their allelopathic effects. Christensen & Muller (1975) reported the dominance of Adenostoma fasciculatum in Chaparral vegetation, which suppressed the seed germination and seedling survival of the neighbouring plant species through allelopathy.

Friedman et al. (1977) reported that volatile and water soluble substances from Artemisia herba-alba strongly inhibited the seed germination of several annuals which showed feeble infestation in close vicinity of the former in Negev desert of Israel. Similarly, Tripathi et al. (1981) found that Trifolium

repens was absent from the close vicinity of Eupatorium adenophorum and they suggested that this may be due partly to the allelochemicals production by E. adenophorum. Rai & Tripathi (1982b) observed that the allelochemicals produced by E. riparium not only reduced the seed germination and seedling growth, but also delayed the germination of several weedy species which in turn might be able to put newly born seedlings in disadvantageous position, especially in stress situations. Putnam & Duke (1974) and Lockerman and Putnam (1979) emphasized the role of allelopathy exhibited by cucumber, in biological suppression of weed population.

Werner (1975) reported that in the field where a near monoculture of quack grass had left 10 - 15 cm litter layer, the few seedlings that were produced (20% of total seeds) died without reproducing while in all other fields germination was relatively high.) Werner & Caswell (1977) also stated that grass litter and the presence of other dicotyledonous species, and the overall primary productivity of the rest of the community are important factors determining the success or failure of an attempted colonization by teasel (Dipsacus sylvestris). Recently a similar report has been made by Sydes & Grime (1981), which showed a negative correlation between the total shoot biomass of ground flora and the amount of leaf litter of several tree species.

Working on the allelopathy of British grasses, Newman & Rovira (1975) observed that out of eight grasses tested by them

four exhibited auto-allelopathy - a mechanism of self regulation of population. A similar behaviour of Blue gramma and Western wheat grass has been reported by Bokhari (1978).

Allelochemics produced by the plants also regulate the population size of rhizospheric microflora (Singh, 1977; Tripathi et al., 1981). Such a change in microbial population might modify various structural and functional attributes of the soil system. For example, Rice (1974, 1977) and Lodhi (1978) observed inhibition of nitrification in grassland and forest community respectively due to presence of allelochemics. These changes in soil system may be expected to result into poor growth of plants growing on such habitats. Recently, Kaminsky (1981) has been able to show that the allelopathic potential of Adenostoma fasciculatum is of microbial origin. Based on the experimental results, he suggested that the role of Adenostoma in the suppression of herb growth may lie in its association with soil microbes that produce and release substances capable of inhibiting the germination and growth of plants.

Effect of herbivores and pathogens : Herbivores and pathogens influence plant distribution (Huffaker, 1964; Harper, 1977), community structure (Harper, 1969) and population growth. In general, herbivore predation reduces the seed and biomass production and increases the level of mortality (Jameson, 1963; Kulman, 1971). While working with a biennial plant species

Dipsacus sylvestris, Werner (1977) observed a reduced seed output from the plants infested by Lepidopteron larvae of noctuid moth (Papaipema catephracta) which feed on the stem pith of teasel. Batra (1979) observed the association of 122 species of insects with Galinsoga ciliata and G. parviflora plants as phytophages or pollinators in Maryland and Guatemala. Based on his visual observation on predation, he suggested that some of these insects, showing preference for capitula and seeds, could be used as biological controlling agent of these weeds. Borchert and Jain (1978) reported the seed predation of annual grasses by rodents in grassland of California while Brown et al. (1979) emphasized the role of granivory in desert ecosystem. Working on the diverse community of winter annuals in the Sonoran desert, Inouye et al. (1980) observed that rodents and ant granivores predated the seeds so much that seedling population density was reduced by 9-fold.

Rausher & Feeny (1980) observed that the pipevine swallow-tail butterfly Battus philenor, consumes 45% of the annual leaf crop of its primary host plant Aristolochia reticulata. They also found that such a devastating effect on foliage-feeding by larvae resulted into greater mortality and decreased growth rate which in turn reduced the seed output. A similar reduction in biomass production and plant survival of Rumex crispus in response to grazing by chrysomelid beetle, Gastrophysa viridula, has been reported by Whittaker (1982) which highlights the role of herbivory in regulation of a

species population. Collins & Aitken (1970) in Trifolium subterraneum and Dirzo & Harper (1980) in Cassella bursa-pastoris observed a substantial delay in the onset of reproduction consequent on defoliation caused by slugs. They also reported a great reduction in seed and biomass production of these plant species due to predation.

The developing and predispersed seed presents an especially nutritious food surface for insects and predation of these seeds is extensive. Platt et al. (1974) investigated the level of predispersed seed predation of Astragalus canadensis by curculionid beetle larvae and reported that about 37% of the pods were attacked in high density arrays vs. 61% in low density arrays. A similar reduction was found for predispersal squirrel predation on ponderosa pine (Larson & Schubert, 1979) and Lepidopteron larvae predation on lupines (Breidlove & Ehrlich, 1972), which depicts the role of predation in regulation of their population size. Working on the shrubby vegetation of California, Louda (1982) reported that the fortnightly application of insecticide during flowering and fruiting reduced the loss of fruits caused by tephritid fly, microlepidopteron moths and chalcidoid wasps from 94% to 41%, thus indicating the role of predators in influencing seed mortality during production.

Pathogens have also a devastating effect on natural ecosystems. Newhook & Podger (1972) reported that the pathogen Phytophthora cinnamoni kills plants in 444 species in 131 genera

of 48 families and has devastated complex forest woodland and heath communities on more than 100,000 hectares in Western Australia. The occurrence of disease like damping-off in Lepidium sativum (Burden & Chilvers, 1975) and stem rot in Eupatorium odoratum (Yadav & Tripathi, 1981) has been reported to contribute to the regulation of their population size in nature. Regehr & Bazzaz (1979) observed that at maturity, 80% of Erigeron canadensis individuals in field populations of Illinois exhibited symptoms of aster yellows, a mycoplasma disease transmitted by the aster leaf hopper (Macrostoteles fascifrons). As a result, seed production was reduced by 53% causing reduction in population size. A similar reduction in growth of Chondrilla juncea consequent on infection by Puccinia chondrillina has been reported by Burdon et al. (1981) which reduces the competitive ability, distribution and abundance of the former in fields of south-eastern Australia.

It is apparent that both 'density-dependent' and 'density-independent' processes hamper the potentiality of plants to increase their numbers geometrically. In spite of this, the populations of many plant species especially the weeds, get widely distributed within a short span of time. Since the weeds compete with the crop plants for various requirements, the attempt is made to remove them from our croplands in order to get optimum yield (Tripathi, 1977). To achieve this end, several weed control practices are adopted. Amongst these, the use of various herbicides and weedicides have proved quite successful

in controlling the weeds. The two weeds selected for the study, Galinsoga ciliata and G. parviflora, grow abundantly both in the cropfields and wastelands of Meghalaya at higher altitudes. An attempt has been made to assess the effect of 2,4-D, the most widely used herbicide for controlling the broad-leaved weeds, on the populations of these two weeds.

The herbicidal sprays have a definite impact on the population dynamics of weed flora. For example, Baker (1972) found that use of hormone-type herbicides results into elimination of annuals and subsequent growth of perennial weeds. Douglas (1965) has also observed a more vigorous growth of Cirsium arvense through vegetative means following a paraquat spray that eliminated its potential competitors. Hanson (1962) reported the transformation of a predominantly broad-leaved weed flora of sugarcane fields of Hawaii into rhizomatous and stoloniferous vegetation due to herbicidal spray. These imply that herbicide activity is species specific and so, before application of herbicide the proper selection is most important.

Kearney (1977) highlighted the importance of environmental factors in influencing the persistence and mobility of herbicides. Helling et al. (1971) observed the poor effect of herbicide mixture on plants growing at moist habitats, whereas Look (1969) reported the lesser effects of 2,4-D on plants grown at microbe-rich soil. Similarly, Blackman & Robert-Cunninghame (1955) and King (1974) reported the better absorption of 2,4-D by plants under bright sunlight and at high temperature.

Mc Ilrath & Ergle (1952) studied the effect of 2,4-D on different stages of development of cotton plant and reported that seedling stage is most susceptible for 2,4-D activity. A similar conclusion has been drawn by Klingman (1953) who studied the effect of different concentrations of 2,4-D on wheat plant. These studies indicate that the herbicide is most effective in weed control when it is applied at seedling stage.

The review of literature reveals that the size of a species population is determined by a number of environmental factors which interact among themselves in a complex manner causing fluctuation in size of a population through change in death and birth rates of individuals.

Review of work done on the Galinsoga spp.

The two species of Galinsoga were recognized by de Candolle in 1836. He separated G. parviflora into two varieties; his G. parviflora var. hispidata is the present day G. ciliata. Rafinesque described it as a new genus and species, Adventina ciliata, in same year, from specimens he found growing in the Bartram Garden of Philadelphia. Bicknell (1916) after examining collection from Nantucket Island, Mass, raised G. parviflora var. hispidata to specific rank and renamed the taxon G. aristulata. Six year later, Blake (1922) rediscovered Rafinesque's publication and placed Bicknell's G. aristulata in synonymy with G. ciliata.

Both species are prolific seeder often producing several thousand seeds per plant. Usami (1976) studied the autoecology of G. parviflora from mulberry fields of Japan and reported that this rapidly growing plant species flowers continuously one month after germination until frost. He also calculated the seed production by a single individual and reported that in Japan each plant may bear 13,400 capitula yielding 400,000 seeds during its life span. He also observed 3-4 generations of these two species in a single year. Ivany & Sweet (1973) studied the behaviour of seeds in G. ciliata and reported that the seeds do not require dormancy and can spread 1.61 km. in 2 years by wind. Salisbury (1942) reported the seed polymorphism in G. parviflora and argued that the ray achenes which constitute 20% of total seed population are larger, flat and devoid of pappus while disc achenes are smaller and crowned with pappus. Recently, Rai & Tripathi (1982c) studied the food reserves of these two seed morphs and reported a significant difference in protein and carbohydrate contents of the seeds. They also found higher energy content in the ray achenes as compared to the disc achenes. The ray achenes also showed better germination from different sowing depths and the seedlings from these grew better under nutrient deficient conditions. They (Rai & Tripathi, 1982c) attributed these differential response of the two achenes to differences in seed reserves and considered it of great adaptive significance.

The cytological studies in the two species was made by Haskell & Marks (1952) in Great Britain and by Chatterjee &

Sharma (1968) in India. They reported that G. ciliata is a tetraploid with chromosome number $2n = 32$ whereas the other species is diploid with 16 chromosomes. Recently, Gopinathan & Babu (1982) studied the cytogenetics of G. parviflora and G. ciliata and their natural hybrids. They recognized four populations; (i) G. ciliata - a segmental allotetraploid $2n = 32$ (ii) G. parviflora - a diploid $2n = 16$ (iii) Triploid natural hybrid between G. parviflora and G. ciliata $3n = 24$, and (iv) Putative introgressant between G. parviflora and the natural triploid hybrid $2n = 16$. They also studied the population size and abundance in Delhi and reported that population (iii) always occurs in smaller size and away from the other populations. Khonglam (1982) reported the presence of accessory chromosomes (i.e. B-Chromosome) in the two species.

Shontz & Shontz (1970) studied the arrival and spread of G. ciliata in north-eastern United States and later they (Shontz & Shontz, 1972a) recognized two ecological races formed over a relatively short period of time in populations growing in Western Massachusetts. Of these, one population grows during summer (outdoor population) while the other grows all through the year (indoor population). Morphological examination revealed that plants of the outdoor population were taller and their seeds were larger than plants of the other population. Seedlings of the indoor population grow slightly better in shade as compared to the outdoor population. Slugs showed preference for outdoor plants. The seeds produced from these populations

also showed specificity for temperature during germination. Seeds from the indoor population were more susceptible to temperature alteration as compared to seeds from the outdoor population. They (Shontz & Shontz, 1972b) also studied the nutrient ecotypes of G. ciliata and found that one population showed more specificity for nutrient as compared to the other, and in nutrient-stressed situation the latter become dominant over the former.

The studies on the herbicidal control of these two weeds was made by Ivany & Sweet (1973) who argued that the herbicidal control of Galinsoga is difficult, although it can be controlled by pre-emergence application of a herbicide, and post-emergence treatment with ammonium nitrate (Stilwell & Sweet (1975)).

Plekhanova et al. (1977) reported that G. parviflora contains triterpene, saponins, tannins, flavonoids and glycosides while G. ciliata young leaves have a peculiar pungent odour, resembling to cedar wood oil. They also reported that these contents in the two species of Galinsoga may influence the composition of the phytophagous insect and other predators fauna attacking them. Batra (1979) studied the insects associated with these two species in Maryland and Guatemala and reported 122 species of insects and one mite as phytophages or pollinators. They have also indicated that some of these insects may be used as biological controlling agents for the two weeds.

Besides being a severe weed of low growing crops, G. parviflora has been reported to be an alternate host of several nematodes (Vinduska, 1967) and primary host of viruses causing tobacco mosaic and cucumber mosaic diseases (Namba & Mitchell (unpublished), quoted in Holm et al., 1977) and of spotted wilt (Sakimura, 1937). It is also reported as host of fungus Ascochyta phaceolorum (Alcorn, 1968).

CHAPTER II

Description of the study site and selected species

STUDY SITE

The study sites (cropland and wasteland) are situated in Shillong (Latitude $25^{\circ}34'N$, Longitude $91^{\circ}56'E$; altitude 1500 m), the capital of Meghalaya state in India. The wasteland site is situated on the campus of the School of Life Sciences, North-Eastern Hill University, while the cropland site is located on the other adjacent hillock where maize and potato were grown during the last three years.

Pot experiments were conducted on the campus of the School of Life Sciences, North-Eastern Hill University, at Nongthymmai, Shillong, under glass-house and net-house conditions.

Climate:

The south-west monsoons and north-east winter winds influence the climate of Shillong. The average rainfall and temperature data are given in Fig. 2.1. The climate is quite wet (annual rainfall being 2500-3000 mm). The months from May to September represent wet season, although occasional showers are received during November to March as well. June and July are the wettest months. The year can be divided into four seasons: (i) Spring (March to April) (ii) Summer (May to September) (iii) Autumn (October to November) (iv) Winter (December to February). The spring season is characterized by gradual increase in temperature over the preceding winter months

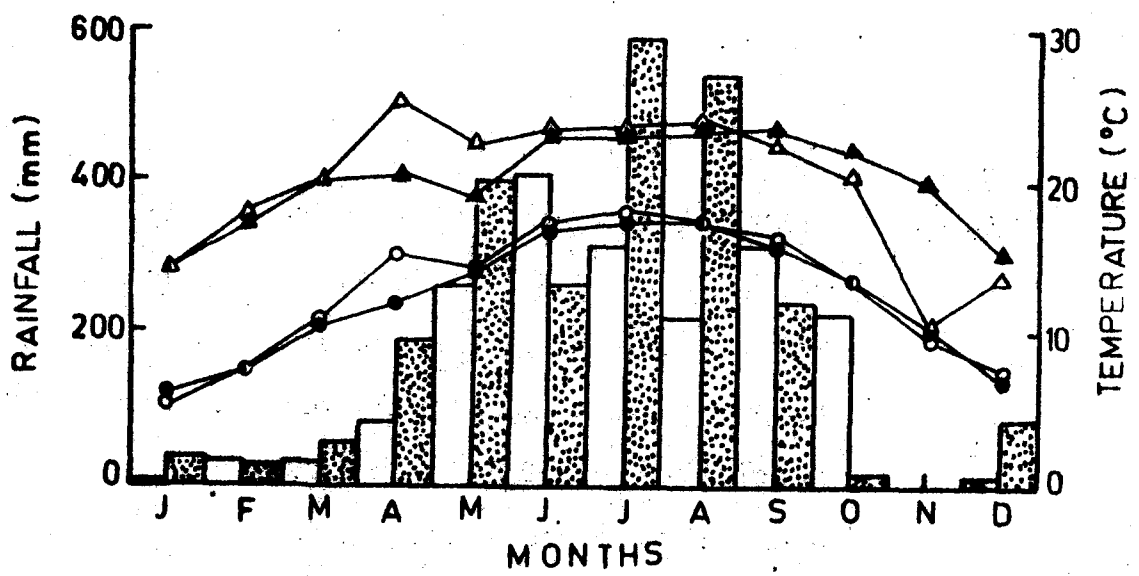


Fig.2.1

accompanied by occasional showers. With further increase in temperature the spring gives way to the summer which is characterized by strong winds (up to May) and abundant rainfall. With the retreat of monsoons, the season changes and fall in temperature heralds the advent of autumn. Autumn is cool followed by winter season lasting from December to February. This period is characterized by low temperature, negligible rains and short photoperiods. Clear winter days are usually followed by frost in the night.

Soil:

The Shillong plateau embracing the Garo, Khasi and Jaintia Hills of Meghalaya is made up largely of pre-cambrian rocks acutely folded and steeply dipping, with an overturned fringe of Mesozoic and Tertiary sediments. The rock distribution in the plateau reveals that the core of plateau is an ancient mass of gneiss much intruded by a coarse granite (Pascoe, 1950). Sandstones, limestones and conglomerates with subordinate clays super-imposed over these rocks also occur in the Shillong plateau (Zimba, 1977). Physical and chemical properties of the top 10 cm soil are shown in Table 2.1. Textural analysis revealed that the soil is silty loam.

Vegetation:

The vegetation of Shillong is characterized by preponderance of evergreen tree species, the commonest of which is

Table 2.1: Physical and chemical properties of soil on the wasteland and cropland sites (values \pm S.E. represent the mean of five samples).

Property	Wasteland	Cropland	Calculated 't'
Porosity (%)	19.8 \pm 1.06	39.0 \pm 1.3	8.81*
Sand (%)	49.2 \pm 1.67	59.2 \pm 2.01	8.02*
Silt (%)	33.0 \pm 1.04	25.6 \pm 1.2	7.20*
Clay (%)	17.8 \pm 1.0	15.2 \pm 0.36	3.11
pH	4.98 \pm 0.12	5.33 \pm 0.10	1.66
Cation-exchange capacity (m.e. per 100 g)	9.92 \pm 1.06	16.3 \pm 1.90	5.90*
Organic matter (%)	3.2 \pm 0.22	5.82 \pm 0.56	4.94*

* Differences significant at $p = 0.01$.

Pinus kesiya. Besides, grasslands are also common. The two weed species selected for the study, Galinsoga ciliata and G. parviflora (Plate 2.1), grow with maize in the hilly agro-ecosystems of Meghalaya (Plate 2.2). They are also associated with Eupatorium riparium and several grass species of disturbed wastelands (Plate 2.3). The common associates of these weeds alongwith their density values are listed in Table 2.2.

SELECTED SPECIES

The two species selected for the present study are Galinsoga ciliata (Raf.) Blake and G. parviflora Cav., the sympatric annual herbs of family Asteraceae. The history of these species can be traced back to 1836 when de Candolle found G. parviflora, and separated it into two varieties. His G. parviflora var. hispida is the present day G. ciliata according to Blake (1922).

Description of the species: (Plate 2.1)

G. ciliata:

It is an erect somewhat flaccid, simple or sparingly branched annual herb, 15-70 cm tall; stems widely branched in the upper part, often decumbent below with simple and glandular hairs in plenty; leaves ovate or elliptic oblong with a cuneate base, acute or rather acuminate, thickly hairy; Flower heads terminal or axillary combined into a terminal, leafy corymbiform panicle; Peduncle short and gland hairy; Ray flowers 5, with white,



G. ciliata

G. parviflora



PLATE 2-1



PLATE 2.2

Plate 2.3: A close up view of wasteland vegetation showing growth of Galinsoga spp. and their associates.



PLATE 23

Table 2.2: List of associates of Galinsoga spp. in cropland and disturbed wasteland habitats with their density values (data based on 10 quadrats, each of 1 m² area).

Plant species	Density	
	Wasteland	Gropland
<u>Arundinella khaseana</u> Nees	18.6	-
<u>Carex cruciata</u> Nees	16.3	-
<u>Cyperus rotundus</u> Linn.	12.3	15.6
<u>Drymeria cordata</u> Willd.	6.6	-
<u>Eupatorium riparium</u> Regel	19.5	-
<u>Eurya japonica</u> Thunb.	3.2	-
<u>Galinsoga ciliata</u> (Raf.) Blake	32.5	61.5
<u>G. parviflora</u> Cav.	14.3	32.8
<u>Hypochaeris radicata</u> Linn.	12.0	-
<u>Oxalis corymbosa</u> DC	3.0	6.8
<u>Panicum indicum</u> Linn.	1.5	-
<u>Paspalum dilatatum</u> Poir	4.6	-
<u>Potentilla mooniana</u> Wight	3.7	-
<u>Pouzolzia hirta</u> Hassk.	-	4.6
<u>Polygonum chinense</u> Linn.	1.3	7.0
<u>Richardia scabra</u> Linn.	-	5.2
<u>Zea mays</u> Linn.	-	7.0

- = indicates species absence.

3-dentate hairy long ligules; corolla of disc flowers yellow hairy and long; Achenes black, hairy, turbinate with 16-20 pappus scales, ciliate pales long, fimbriate and acute.

The species is often confused with G. parviflora but it is easily recognizable by awn-tipped pappus scales, longer ligules of ray flowers, entire pales and densely glandular hairy stems and peduncles.

G. parviflora:

It is an erect slender, soft often branched annual herb, 20-100 cm tall; stem either with minute hairs or smooth; Root is shallow and fibrous; leaves opposite, simple, three prominent nerves with wedge-shaped (cuneate) base and tapering blunt or pointed apex; Petiole long; Flower head small; The ray flowers white, five in number, 3-lobed bracts of two series, membranous; Fruit (achene) black, angled or the other ones flat widening upward, pappus of numerous persistent scales.

The distinguishing characteristics of this weed are the usually five, small, white, outer ray florets and the yellow central disc florets, plus the absence of a pappus on the seeds of the ray florets.

Distribution and habitat:

The genus Galinsoga comprising 14 species (Cannie, 1977) is native to the mountains of tropical America but has now been

spread throughout much of the world, including tropical lowland South and central America. The two species (i.e. G. ciliata and G. parviflora) are reported from India (Babu, 1969), China (Chi-chu et al., 1975), Japan (Usami, 1976), Java (Martin & Ruberte, 1975), Australia (Herbert, 1939), Europe (Lascombe, 1964), Finland (Kaantonen, 1976) and Canada (Frankton & Mulligan, 1970). Holm et al. (1977) reported that the plant of G. parviflora grows from about 54°N latitude to 40°S as a weed of 32 crops of 38 countries. However, in hilly regions of India it grows as a subordinate species together with dominant G. ciliata (Babu, 1977).

Both species, besides being the weeds of ruderal habitats, occur as cropweeds in agro-ecosystems at high altitudes. In New York, both species are severe problems in low growing vegetable crops that do not shade the soil surface, such as cole and salad crops (Ivany & Sweet, 1973). They rank 33rd among the 50 most important weeds in horticultural crops in the entire United States, and are common in the fields with vegetables and small fruits in the north-east (Danielson et al., 1965; Jansen et al., 1972).

The plants of the two weeds grow best in moist conditions and can become very abundant under irrigation or year round rainfall in the tropics. Although these species are weeds of the early growing season, the plant is very susceptible to **frost** injury and are often the first to succumb in the fall (Holm et al., 1977).

CHAPTER III

Population dynamics of different seedling cohorts
of G. ciliata and G. parviflora at two contrasting
sites

INTRODUCTION

Any study on population dynamics involves the quantification of the birth, death, immigration and emigration rates of a species population, and it also seeks to explain the changes in time and space that occur in these parameters. The population dynamics of several perennial grasses and herbs has been studied by Williams (1970), Antonovics (1972), Sarukhan & Harper (1973), Hawthorn & Cavers (1976), Bishop et al. (1978), Yadav & Tripathi (1981) and Law (1981) and of biennials by Holt (1972) and Klemow & Raynal (1981). However, the population dynamics of annual plant species are least known although they pose relatively lesser practical problems (Harper & White, 1974). Some of the works done on annuals are those by Sharitz & Mc Cormick (1973) who studied the population dynamics of Sedum smallii and Minuartia uniflora, and by Watkinson & Harper (1978) on Vulpia fasciculata. Recently, Weiss (1981) studied the population dynamics of Emex australis.

The cropland and wasteland habitats where the two weeds, G. ciliata and G. parviflora, grow abundantly differ markedly from each other in respect of several ecological factors (Table 2.1). Due to lack of dormancy in seeds (Ivany & Sweet, 1973) and with short life cycle, the seedling cohorts of the two weeds keep on appearing in nature at different time intervals subject to favourable temperature and moisture conditions (Usami, 1976). The analysis of survival of different cohorts of a species

population developing at different times seems to be essential for complete understanding of the population behaviour of the species. The present study, therefore, aims at analysing the population behaviour of different seedling cohorts of these two weeds as related to habitat conditions.

MATERIALS AND METHODS

For demographic studies, six permanent 0.25 m^2 quadrats were randomly laid in $2.5 \times 9 \text{ m}^2$ area, chosen subjectively to give an almost similar density of plants in each quadrat on both wasteland and cropland sites. The seedling emergence, survivorship and reproductive growth of the two species populations were studied in the permanent quadrats from April 1980 to December 1981. Both species have three seedling cohorts appearing in different months. These cohorts (described as cohorts I, II and III) were marked in late April, mid May and Mid August in 1980 and mid March, mid April and late July in 1981 with the help of waterproof British paint of different colours. Each seedling was marked with a dot of paint on the tip of its first leaf. The fate of the seedling cohorts was followed at fortnightly intervals from emergence until death and the time taken from emergence to 50% survivorship was calculated as half life. The density of the associates of Galinsoga present in the permanent quadrats on the two sites was recorded (Table 3.1), which showed nine-fold increase in density from April 1980 to 1981, which in turn intercepted 20%

Table 3.1: Major associates of Galinsoga spp. and their density per 0.25 m² (±S.E.) observed in the permanent quadrats in April 1980 and April 1981.

Plant species	1 9 8 0		1 9 8 1	
	Wasteland	Cropland	Wasteland	Cropland
<u>Ageratum conyzoides</u>	-	0.3 \pm 0.3	-	8.3 \pm 1.2
<u>Carex cruciata</u>	1.0 \pm 0	-	1.0 \pm 0	-
<u>Cyperus rotundus</u>	1.3 \pm 0.6	1.3 \pm 0.3	1.0 \pm 0	13.3 \pm 0.3
<u>Oxalis latifolia</u>	2.0 \pm 0	-	2.6 \pm 0.3	-
<u>O. corymbosa</u>	1.0 \pm 0	1.0 \pm 0	1.6 \pm 0.3	3.6 \pm 0.6
<u>Panicum indicum</u>	1.0 \pm 0	-	1.0 \pm 0	7.3 \pm 1.6
<u>Polygonum chinense</u>	1.3 \pm 0.3	1.3 \pm 0.6	2.0 \pm 0	4.0 \pm 0
<u>Pouzolzia hirta</u>	-	0.3 \pm 0.3	-	6.0 \pm 1.2
<u>Richardia scabra</u>	-	1.3 \pm 0.3	-	5.3 \pm 0.8
<u>Rumex nepalensis</u>	-	-	1.0 \pm 0	13.6 \pm 0.3
<u>Setaria palmifolia</u>	2.0 \pm 0	-	2.0 \pm 1.2	4.0 \pm 0
<u>Trifolium repens</u>	4.3 \pm 0.3	-	3.3 \pm 0.3	-
<u>Triumfetta rhomboidea</u>	-	-	-	3.3 \pm 0.6
<u>Zea mays</u>	-	2.0 \pm 0	-	-
<u>Galinsoga</u> spp.	437.6 \pm 39	500.3 \pm 17	307.0 \pm 23	252.0 \pm 38

- = indicates species absence.

of total sunlight on the cropland site.

Number of fertile plants per unit area, number of seeds per plant and percentage contribution of each cohort to the total seed output were also estimated. In each year at the time of maturity, 10 to 18 plants from each of the three cohorts of both species were collected from the areas adjacent to the permanent quadrats and were brought to the laboratory to estimate the seed output and dry matter production. The number of seeds produced by a plant was estimated by multiplying the mean number of capitula per plant by the number of seeds per capitulum. The biomass was estimated after drying the plant material in a hot air oven at 60°C for 48 h. The seed weight per g biomass i.e. crude reproductive effort (CRE, Harper & Ogden, 1970) was calculated for each cohort of either species.

In order to investigate the seed source that gave rise to the III cohort which appeared about 3 months after the II cohort, soil seed population of Galinsoga spp. was estimated at bimonthly intervals from February 1981 to December 1981. Both species were considered together because it was impossible to distinguish the seeds of two species recovered from soil as they are of similar morphology. The soil seed population was estimated by taking five 10 x 10 x 5 cm soil samples from areas adjacent to the permanent quadrats on the two sites. The soil was air dried and seeds of Galinsoga spp. were sorted out with hand and counted. The sorting of any given lot was done twice to ensure accuracy in seed recovery.

RESULTS

Life cycle attributes:

Seeds of Galinsoga germinate in March and April (spring) when the temperature rises and the first rains are received. In 1980, three germination flushes (in April, May and August) were observed on both the sites, thus giving three distinct seedling cohorts. The plants from the I and II cohorts developed to flowering and seeded in June/July. A fraction of these seeds gave rise to the III cohort of seedlings in August 1980, which is evident from the loss of a large fraction of original seed bank in soil before the emergence of the III cohort (Table 3.2).

Table 3.2: Galinsoga seed population (\pm S.E.) per 0.25m² of soil in wasteland and cropland situation during 1981 (both species considered together),

Site	Observation dates					
	3 Feb.	4 Apr.	2 Jun.	1 Aug.	12 Oct.	3 Dec.
Wasteland	1095 \pm 98.4	302 \pm 18	26 \pm 6.7	483 \pm 26.3	1112 \pm 56	1268 \pm 59
Cropland	2438 \pm 215	715 \pm 20.2	12 \pm 3.1	312 \pm 39	996 \pm 102	915 \pm 92

The III cohort completed its life cycle in November. No seedling emergence and plant survival of Galinsoga spp. was noticed in the quadrats during January and February due to severe cold. In 1981 as well, the same cycle was repeated except the time of seed germination which was preponed by one month due to relatively higher rainfall received during March and April.

Seedling emergence:

In the cotyledonary stage, since it was difficult to distinguish the seedlings of the two weeds, their seedlings were counted together until the first leaf stage. Later on, the seedlings of the two species were counted separately. On both cropland and wasteland sites, the first seedling cohorts which appeared in April 1980 and March 1981 were quite large while the II and III seedling cohorts were smaller (Table 3.3). Like seedling emergence, the total density of Galinsoga also remained fairly high on the cropland site compared with wasteland during first year of study but the reverse trend was observed in the following year (Fig. 3.1). The pattern of seedling emergence differed little in 1980 and 1981 but the number of seedlings emerged in 1980 was greater than in 1981 on both the sites (Table 3.3).

Survivorship of seedling cohorts:

On both the sites, the cohorts emerging in 1980 showed longer half life and survived better than those emerging in 1981 (Table 3.3). On the cropland site, half life of the I cohort was 6.2.5 times longer than that on the wasteland site in 1980. In 1981, the I and II seedling cohorts had longer life span than the III cohort, while in preceding year there was little difference in half life of the cohorts emerging at different times.

Table 3.3: Density and half-life (\pm S.E.) of seedling cohorts of Galinsoga spp. emerging at different times in permanent quadrats (both species considered together).

Site	Date cohort was first observed	No. of seedlings/ 0.25 m ²	Half-life (weeks)
Wasteland	26 April 1980	437.6 \pm 39	3.1 \pm 0
	18 May 1980	39.3 \pm 2.6	3.1 \pm 0.3
	20 August 1980	128.6 \pm 17.9	3.5 \pm 0.3
	10 March 1981	405.3 \pm 18.8	2.9 \pm 0.3
	20 April 1981	155.0 \pm 7.8	2.2 \pm 0
	12 July 1981	110.6 \pm 9.3	1.6 \pm 0
Cropland	28 April 1980	500.3 \pm 17	7.9 \pm 0.6
	19 May 1980	137.6 \pm 31.8	3.0 \pm 0
	22 August 1980	201.0 \pm 27.4	3.0 \pm 0.6
	18 March 1981	335.0 \pm 21.6	2.0 \pm 0
	20 April 1981	106.0 \pm 15.9	2.0 \pm 0.2
	27 July 1981	81.3 \pm 7.5	1.4 \pm 0.3

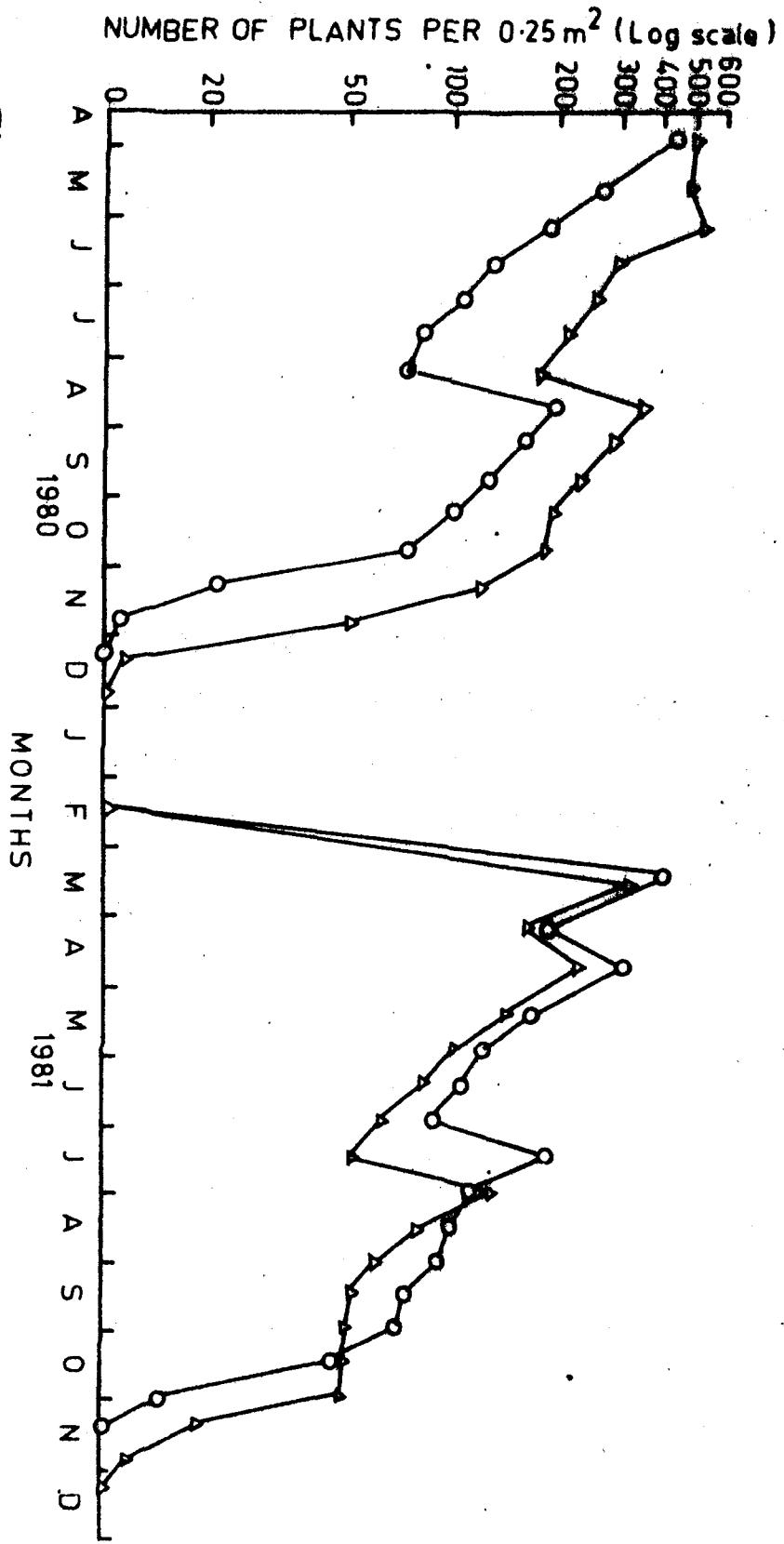


Fig. 3.1

The cohorts of both species marked in April 1980 in wasteland experienced greater mortality than in cropland (Fig. 3.2 & 3.3). In wasteland, out of 132 and 92 established plants of G. ciliata and G. parviflora respectively only 52 and 18 plants survived and produced seeds while in cropland the proportion of surviving and reproducing population was higher. On the contrary, in 1981 relatively greater survival and reproductive growth was observed on wasteland (Fig. 3.2 & 3.3; Table 3.4 & 3.5).

Although the II cohorts of both weeds were smaller, they showed relatively poor survival as compared to the I cohorts (Fig. 3.2 & 3.3). In 1981, no plant from the II cohort of G. parviflora survived up to flowering stage in both wasteland and cropland while in the cropland in 1980 only 8% of the plants survived up to flowering (Table 3.5).

The III seedling cohorts of the two species differed from the earlier cohorts in respect of survival and reproduction. The III cohort of G. ciliata showed heavier mortality than the earlier cohorts especially on cropland site where all the plants recruited in 1981 died before flowering (Fig. 3.2, Table 3.4). Conversely, the III seedling cohort of G. parviflora survived and reproduced better as compared to II cohort especially in the wasteland where all the plants from the II cohort died in juvenile phase (Fig. 3.3). However, the I cohort did better as compared to the III cohort on both the

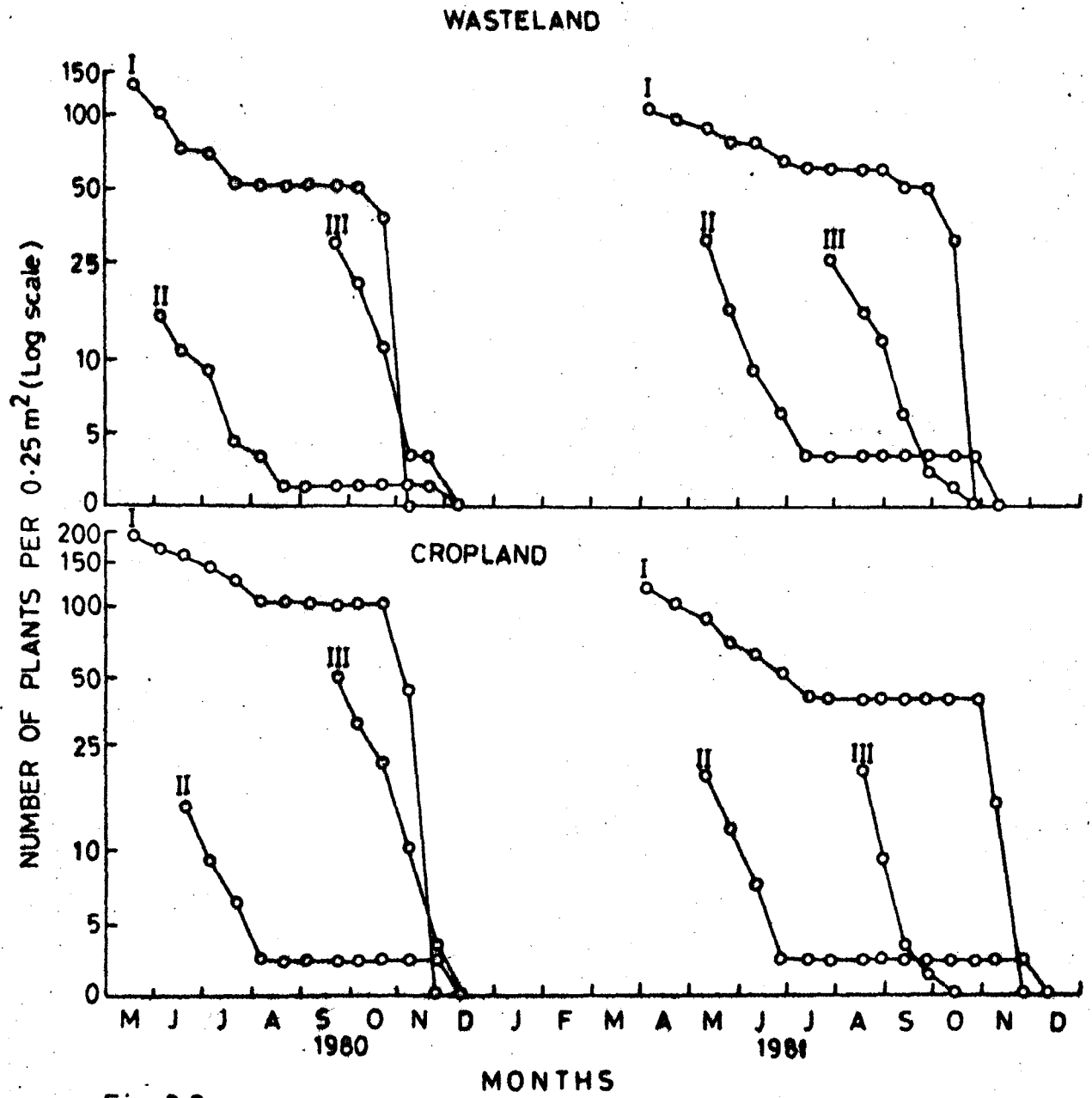


Fig. 3.2

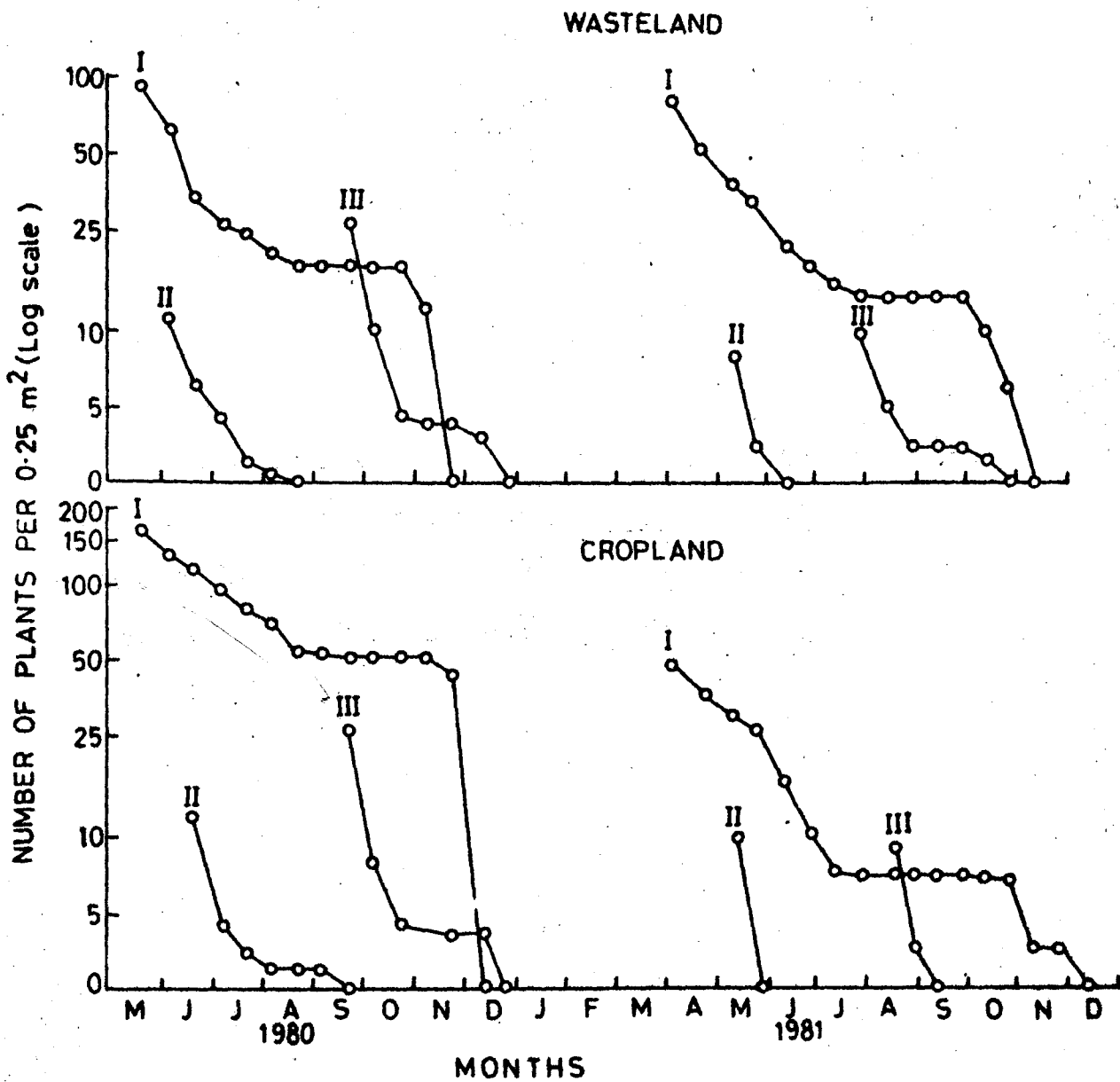


Fig. 3-3

Table 3.4: Reproductive behaviour of the three seedling cohorts of *G. ciliata* emerging at different times in wasteland and cropland. (\pm S.E.).

Site and growing year	Seedling cohort	Number of flowering plants per 0.25m^2	Number of seeds per plant	Crude reproductive effort (CRE)	
Wasteland	1980	I	52.0 \pm 2.8 ^{a*}	56.8 \pm 2.8 ^a	17.7 \pm 1.6 ^a
		II	1.0 \pm 0.0 ^e	60.0 \pm 3.4 ^a	20.0 \pm 2.0 ^a
		III	3.0 \pm 0.5 ^f	16.2 \pm 1.6 ^b	10.9 \pm 2.3 ^c
	1981	I	62.0 \pm 4.0 ^b	66.0 \pm 2.6 ^c	19.3 \pm 1.2 ^a
		II	3.0 \pm 0.5 ^f	59.8 \pm 3.3 ^a	22.8 \pm 1.6 ^b
		III	1.0 \pm 0.5 ^e	35.0 \pm 2.3 ^d	14.6 \pm 1.3 ^d
Cropland	1980	I	100.0 \pm 4.6 ^c	101.7 \pm 8.3 ^e	20.0 \pm 1.6 ^a
		II	2.0 \pm 0.0 ^e	115.0 \pm 4.6 ^f	22.6 \pm 2.3 ^b
		III	3.0 \pm 1.3 ^f	22.4 \pm 3.2 ^b	11.5 \pm 0.6 ^c
	1981	I	40.0 \pm 3.4 ^d	102.2 \pm 7.8 ^e	21.8 \pm 2.7 ^b
		II	2.0 \pm 0.6 ^e	94.5 \pm 6.6 ^e	22.6 \pm 2.3 ^b
		III	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^g

* Means in each column followed by the same letter are not significantly different ($P > 0.05$).

Table 3.5: Reproductive behaviour of the three seedling cohorts of G. parviflora emerging at different times in wasteland and cropland (\pm S.E.).

Site and growing year	Seedling cohort	Number of flowering plant per 0.25 m ²	Number of seeds per plant	Grade reproductive effort (CRE)	
Wasteland 1980	I	18.0 \pm 0.8 ^{a*}	152.0 \pm 6.8 ^a	14.6 \pm 1.6 ^a	
	II	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^f	0.0 \pm 0.0 ^d	
	III	3.6 \pm 0.6 ^e	90.0 \pm 7.3 ^d	9.6 \pm 1.3 ^c	
	1981	I	14.0 \pm 2.5 ^c	135.0 \pm 6.2 ^e	13.6 \pm 1.6 ^a
		II	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^f	0.0 \pm 0.0 ^d
		III	2.0 \pm 0.6 ^f	88.0 \pm 6.2 ^d	8.3 \pm 1.3 ^c
Cropland 1980	I	52.0 \pm 2.3 ^b	221.0 \pm 14.8 ^c	15.0 \pm 2.3 ^a	
	II	1.0 \pm 0.6 ^f	164.0 \pm 6.7 ^a	11.7 \pm 1.3 ^b	
	III	3.3 \pm 1.1 ^e	154.9 \pm 4.9	10.5 \pm 1.5 ^b	
	1981	I	7.0 \pm 2.4 ^d	59.0 \pm 6.2 ^e	11.2 \pm 1.6 ^b
		II	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^f	0.0 \pm 0.0 ^d
		III	0.0 \pm 0.0 ^g	0.0 \pm 0.0 ^f	0.0 \pm 0.0 ^d

* Means in each column followed by the same letter are not significantly different ($P > 0.05$).

sites. In cropland, the III cohort of G. parviflora survived better with 13% of the individuals reproducing in 1980 but in the following year, the survival was nil.

In general, both weeds exhibited almost similar survival pattern with greater mortality risk during seedling establishment and senescent phase. However, G. ciliata experienced lesser mortality than G. parviflora on both the sites before senescence (Fig. 3.2 & 3.3).

Reproductive behaviour:

In both species the number of fertile plants declined from the first to second year except in case of the I and II cohorts of G. ciliata on the wasteland (Table 3.4). The decrease was, however, more pronounced in G. parviflora (Table 3.5). In cropland relatively more fertile plants were observed in 1980, but in 1981 the fertility of the two weeds was greater on the wasteland. In 1980, per plant seed output and CRE of both weeds were relatively greater in cropland than in wasteland, but in the following year the reverse trend was observed in G. parviflora. In case of G. parviflora seed output and CRE decreased from 1980 to 1981 while in G. ciliata the values showed little differences (Table 3.4 & 3.5). The maximum CRE was exhibited by the II cohort in G. ciliata and by I cohort in G. parviflora. The I cohort of both species contributed maximum to the total seed output (Table 3.6).

Table 3.6: Percentage contribution of the different cohorts to the total seed output per unit area of G. ciliata and G. parviflora in wasteland and cropland.

Site and growing year	<u>G. ciliata</u>			<u>G. parviflora</u>		
	I	II	III	I	II	III
Wasteland						
1980	96.5	22.0	1.5	89.4	0.0	10.6
1981	95.0	4.2	0.8	91.5	0.0	8.5
Cropland						
1980	97.2	2.2	0.6	94.5	1.3	4.2
1981	95.6	4.4	0.0	100.0	0.0	0.0

DISCUSSION

The population density of both Galinsoga spp. was highest in spring, due to large flush of germination and seedling emergence. The density either remained constant or declined in the first year of study as the mortality of the spring cohort was either equal or greater than the rate at which new seedlings emerged later. In the following year, the II cohort also exhibited comparatively high density although it was smaller than the I cohort (Table 3.3). The II cohort was smaller in size, due to depletion of seed bank in soil (Table 3.2) after the germination of most seeds in spring. By July-August in both years, the over-all density increased once again (Fig. 3.1) as the seeds produced by the I and II cohorts gave rise to the seedlings of III cohort. Later on, as the winter approached in December, the density declined drastically and reached to zero which indicates the role of lower temperature in influencing the populations of the two weeds. The lower temperature during winter, besides causing plant death also checked the seed germination in spite of large seed bank in the soil. Similar response to cold has been observed by Raynal & Bazzaz (1975b) in some other annuals.

The change in density was also influenced by biotic factors which affected both the rate of emergence and mortality. The seedling cohorts emerging in 1981 were smaller than those in 1980 especially in the cropland (Table 3.3). In spite of fairly high seed population in soil, the seed germination was

poor on cropland site in 1981, which may be attributed to an increased density of the associates. This is in agreement with the findings of Tamm (1956) and Singh (1980) who observed poor recruitment and establishment of seedlings in established communities.

The greater mortality risk in both weeds during juvenile phase is in conformity with the findings of Sharitz & Mc Cormick (1973) who concluded that high mortality during seedling establishment is common in colonizing species which showed high reproductive potential. Mack (1976) and Watkinson & Harper (1978) have emphasized the occurrence of Type II and Type III survivorship curve (Deevey, 1947) in species capable of producing large number of seeds in contrast to those which produced lesser number of seeds and exhibited the Type I survivorship curve. Although earlier workers (Antonovics, 1972; Harper, 1977; Johnson & Thomas, 1978) have demonstrated that survival of herbaceous plants is generally a linear function of time, the present study illustrates the occurrence of both linear (Type II) and concave (Type III) survivorship curves. The enhanced mortality during active growth phase of the two weeds could be probably related to increased resource competition rather than climatic events which were not harsh during the active growth phase. Sarukhan & Harper (1973), Hawthorn & Cavers (1976) and Yadav & Tripathi (1981) have also attributed high mortality during active growth phase to increased competition for resources.

Survival of the late arriving cohorts may be adversely affected by the already established individuals of the spring cohorts of the two weeds. The spring cohorts showed relatively greater survivorship and half life in spite of larger size, indicating that the population regulation in this case may be density-independent as also argued by Klemow & Raynal (1981) in Melilotus alba. The greater survival of early emerging cohort of G. ciliata relative to the other cohorts conforms with the population behaviour of certain other species studied by Sarukhan & Harper (1973), Hawthorn & Cavers (1976), Weaver & Cavers (1979) and Weiss (1981). However, the III cohort of G. parviflora which appeared later than the II cohort showed better survival. This behaviour may probably be attributed to fluctuation in degree of interference from the well suited I and II cohorts of the co-existing G. ciliata, which offered more keen competition during active phases of life when the II cohort of G. parviflora appeared, but later on i.e. at the time when the III cohort appear, the co-existing individuals which had undergone passive growth phase might offer reduced competition.

In 1980, both weeds showed longer half life and greater survival and seed production in the cropland situation than in the wasteland, which could probably be attributed to lesser competition from the associates which had lower density in the former situation. The seedling mortality was much greater in 1981 probably due to increased density of the associates

(Table 3.1) which reduces the light available to the seedlings by c. 20%. Putwain & Harper (1970), Raynal & Bazzaz (1975b) and Tripathi & Dwivedi (1978) reported that the distribution and abundance of a species may be profoundly modified by the presence of associated species in community. The seedlings of both weeds were also damaged by slugs which occur in great abundance during peak rainy season, indicating the possible role of predation in the seedling survival of these weeds.

The year-wise increase or decrease in total seed output of G. ciliata on the two sites was mainly due to change in number of fertile plants rather than change in seed output per plant, while G. parviflora showed reduction in per plant seed output due to individual plastic response to density. In contrast to findings of Weaver & Cavers (1979), per plant seed production and CRE of the later emerging cohort was lower as compared with the early emerging cohort. However, the CRE of the two species did not vary much with the year indicating that the energy allocation to reproductive purposes remains unaffected by the high density of associates in 1981. Constancy in reproductive allocation has also been reported by Harper & Ogden (1970) and Raynal & Bazzaz (1975b) in certain other annuals grown under various degree of stress.

G. ciliata and G. parviflora may be regarded as fugitive species in that they typically prefer disturbed and open sites to grow better and to produce more seeds which enable them to invade new disturbed habitats. They also occur in fields lying

abandoned for a year, but they are suppressed considerably due to growth of other associated plant species on such sites. The emergence of different seedling cohorts at different time periods in both weeds may be viewed as an important strategy in so far as the maintenance of the populations is concerned. It reduces the degree of intra-and inter-specific competition by avoiding crowding at the same time. The occurrence of more than one seedling cohorts may also ensure the successful completion of the life cycle of some cohort or the other in case the environmental conditions prevailing during the life time of a particular cohort prove to be too rigorous to render the survival really precarious.

CHAPTER IV

The regulation of G. ciliata and G. parviflora populations:

- a) Effect of associated vegetation on the sown seeds and transplants of the two Galinsoga spp.
 - b) Allelopathic effect of E. riparium on seed germination and growth of the two Galinsoga spp.
 - c) Effect of established populations of G. ciliata and G. parviflora on their late emerging seedling cohorts
-

- a) Effect of associated vegetation on the sown seeds and transplants of the two Galinsoga spp.

INTRODUCTION

In field situation, the success of a species population is largely determined by the associated plant species growing in its proximity (Raynal & Bazzaz, 1975a; Tripathi & Dwivedi, 1978). Relatively poor recruitment of seedlings from seeds in established plant communities has been reported by Tamm (1956), Cavers & Harper (1967), Putwain & Harper (1970) and Singh (1980). Cavers & Harper (1967) observed that some of the phytometers of Rumex acetosa and R. obtusifolius introduced in established community could survive and grow for longer duration as compared to the individuals originating from the sown seeds. Similarly, Chippindale (1948) suggested that seedlings of the grasses can survive for long duration in swards but without showing increase or loss in biomass. These studies illustrate the significant role played by the established vegetation on population growth of a species placed in that situation. Thus, a study pertaining to the effect of established plant populations on seed germination, survivorship and growth of young seedlings of the two species of Galinsoga was undertaken.

MATERIALS AND METHODS

The study site was an eastward facing slope, situated on the campus of the School of Life Sciences, North-Eastern

Hill University, Shillong. The experiment was carried out on the top of the slope. The vegetation of the study plot comprised of Eupatorium adenophorum and E. riparium as dominant herb layer. The other major plant species present on the site are given in Table 4.1 alongwith their densities. One half portion of the study plot was cleared of all the vegetation while the other half was left as it is i.e. without removing the plants. Freshly collected mature seeds of G. ciliata and G. parviflora were sown in the study plot at the rate of 400 seeds per 0.25 m^2 on 10 May 1981. A census of the seedlings was done after a fortnight from sowing. On the same date 40 seedlings of 4 leaf stage were transplanted in the other set of 0.25 m^2 subplots representing both cleared (vegetation free) and uncleared (vegetation not removed) plots to study the effect of associated vegetation on the young transplants of the two weed species. The initial growth parameters of the seedlings and transplants were measured on 25 May 1981. 36 subplots of $50 \times 50 \text{ cm}$ were maintained for each species to allow three harvests in three replicates for each of the two treatments of seed born seedlings and transplants.

Observations were made on survivorship of the seedlings at about fortnightly intervals. (The other observations like leaf area, biomass production and seed output per plant were estimated by harvesting the 15 plants from each treatment after 6, 12 and 18 weeks from first census/planting date. The biomass of the plants was estimated by the procedure described by Misra (1968).)

Table 4.1: List of common plant species with their densities per m² on the study site where the vegetation was not removed (Data based on 10 quadrats of 1 m²).

Species	Density (\pm S.E.)
<u>Eupatorium adenophorum</u> Spreng.	16.8 \pm 3.5
<u>E. riparium</u> Regel	13.6 \pm 2.5
<u>Drymaria cordata</u> Willd.	6.2 \pm 0.6
<u>Eurya japonica</u> Thunb.	8.5 \pm 1.2
<u>Panicum brevifolium</u> Roxb.	16.3 \pm 2.1
<u>Potentilla mooniana</u> Wight	4.8 \pm 0.3
<u>Osbeckia crinata</u> Benth.	13.5 \pm 1.6
<u>Arundinella khaseana</u> Nees	20.8 \pm 2.9
<u>Hypochoeris radicata</u> Linn.	12.0 \pm 1.2

Table 4.2: Number of seedlings per 400 seeds sown on the cleared and uncleared plots and reduction in seedling emergence caused by the associated vegetation (\pm S.E.)

Species	No. of seedlings emerged		Percentage reduction in seedling population
	Without associates	With associates	
<u>G. ciliata</u>	209 \pm 24	145 \pm 28	30.6 \pm 8.6
<u>G. parviflora</u>	185 \pm 13	89 \pm 12	51.9 \pm 11.8

RESULTS

Seed germination:

Seed germination of the two Galinsoga species was considerably reduced due to presence of the associated vegetation (Table 4.2). However, the reduction in seed germination was more pronounced in G. parviflora than in G. ciliata.

Survivorship:

The survivorship of the seed born seedlings and transplants of both species was substantially reduced due to the presence of associated vegetation (Fig. 4.1). The seedling populations of both species especially G. parviflora decreased drastically during active growth phase. In G. parviflora the seedlings allowed to grow with the associates showed almost nil survival. On the contrary, survivorship of the seedlings was very high in the plots devoid of vegetation. The mortality rate, as indicated by the survivorship data, was lower in transplants of the two weeds as compared to that of seed born seedlings. However, G. ciliata showed better survivorship than G. parviflora and c.5% seed born seedlings and 15% transplants survived over the whole study period.

Leaf area per plant:

The presence of associated vegetation caused substantial reduction in leaf area per plant of the two Galinsoga spp. The suppression was more severe in case of G. parviflora than in

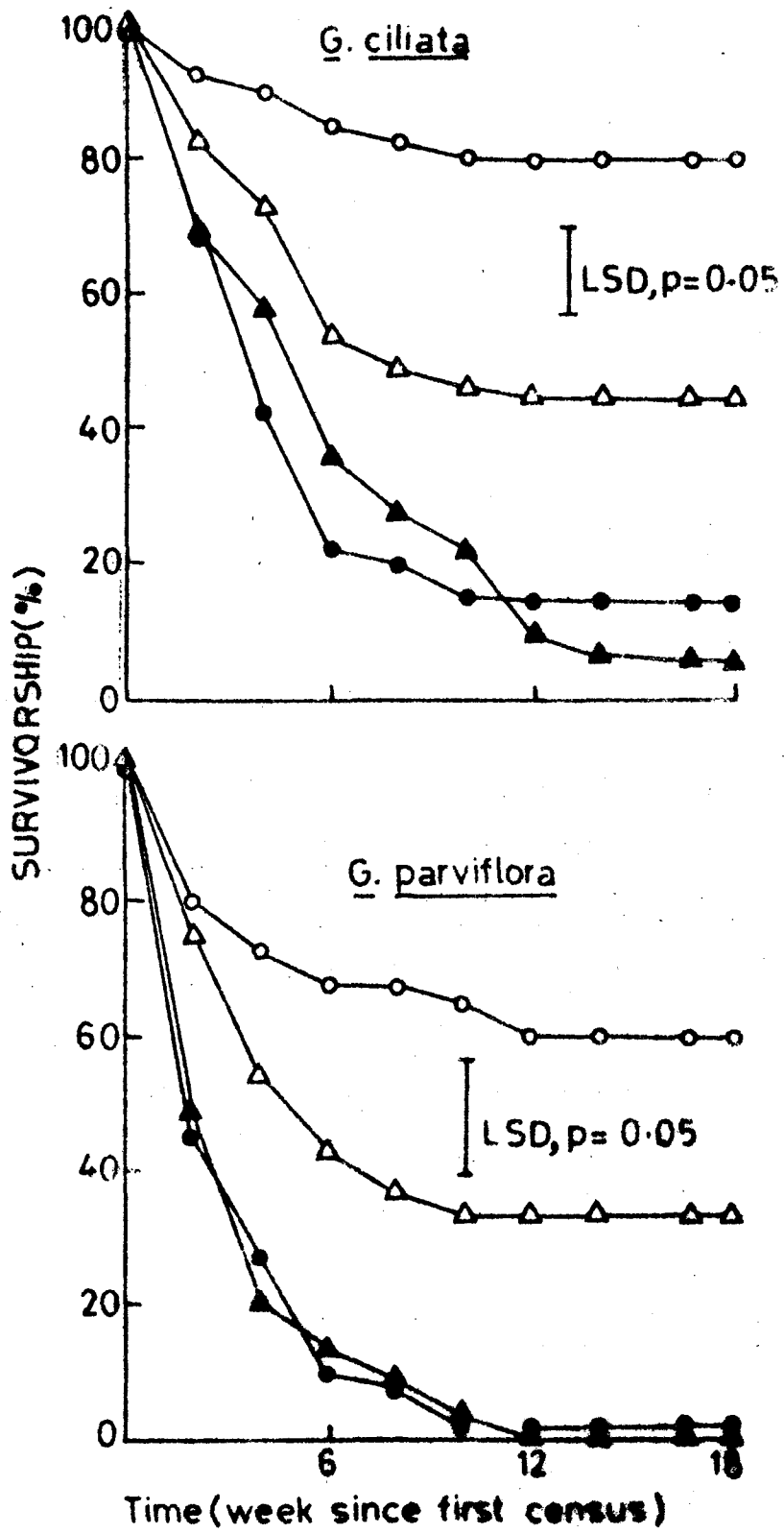


Fig. 4.1

G. ciliata (Fig. 4.2, Plate 4.1A & 4.1B). However, the transplants of the two weeds showed relatively greater leaf area than the seed born seedlings.

Biomass per plant:

The yield per plant of the two species of Galinsoga was also greatly reduced in the presence of associated vegetation (Fig. 4.3, Plate 4.1A & 4.1B). The decrease in yield was more conspicuous in G. parviflora than in G. ciliata. Biomass of the two species showed only slight increase with time in presence of the associates while in absence of associates it increased substantially. Like other parameters, biomass of the transplants was also greater than that of the seed born seedlings.

Reproductive growth:

None of the seed born seedlings of the two weedy species produced flowers when grown with the associated vegetation while in the study plots devoid of vegetation, the seedlings of the two species showed good reproductive growth and produced enormous number of seeds (Table 4.3). This clearly indicates that the presence of the associated vegetation caused drastic reduction in reproductive growth of the Galinsoga spp. However, the transplants of the two weeds were better adapted to this situation and produced larger number of seeds than the seed born seedlings.

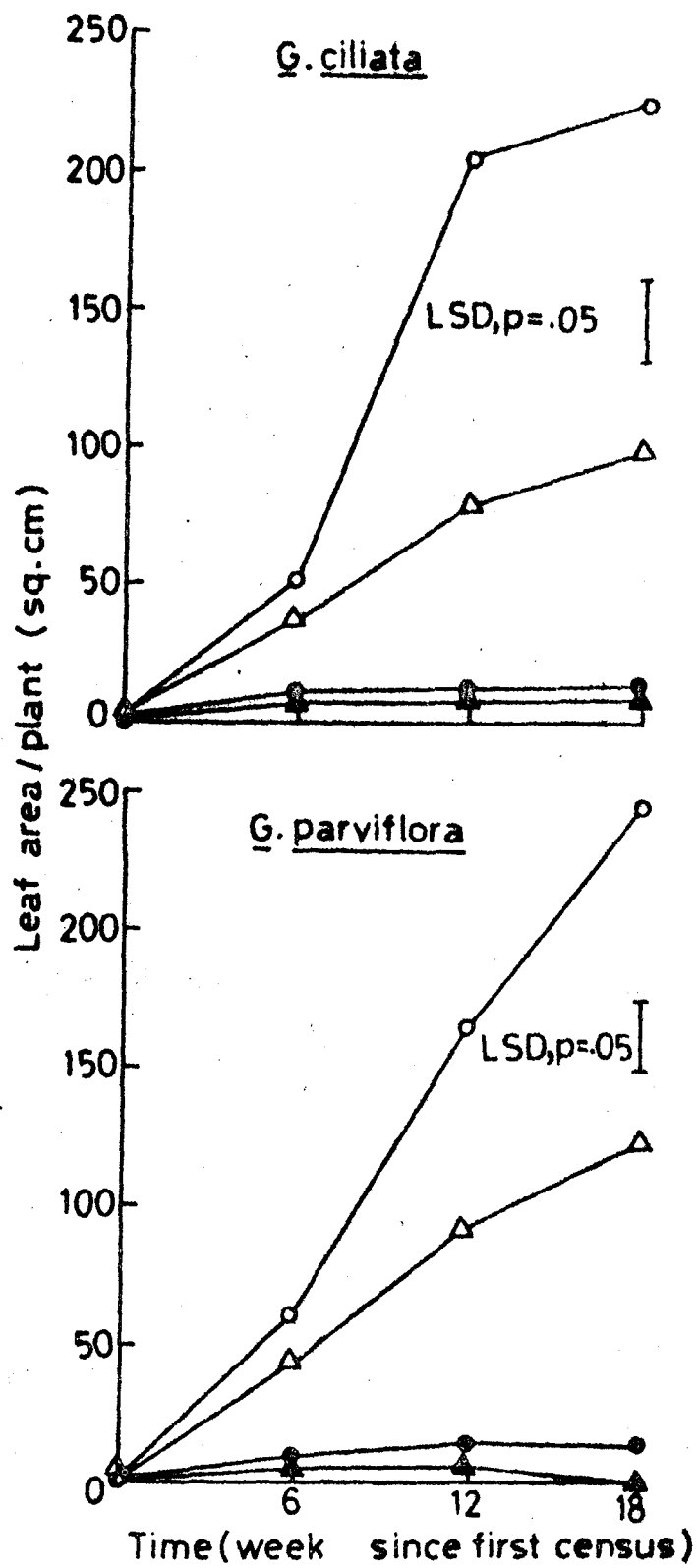


Fig. 4.2

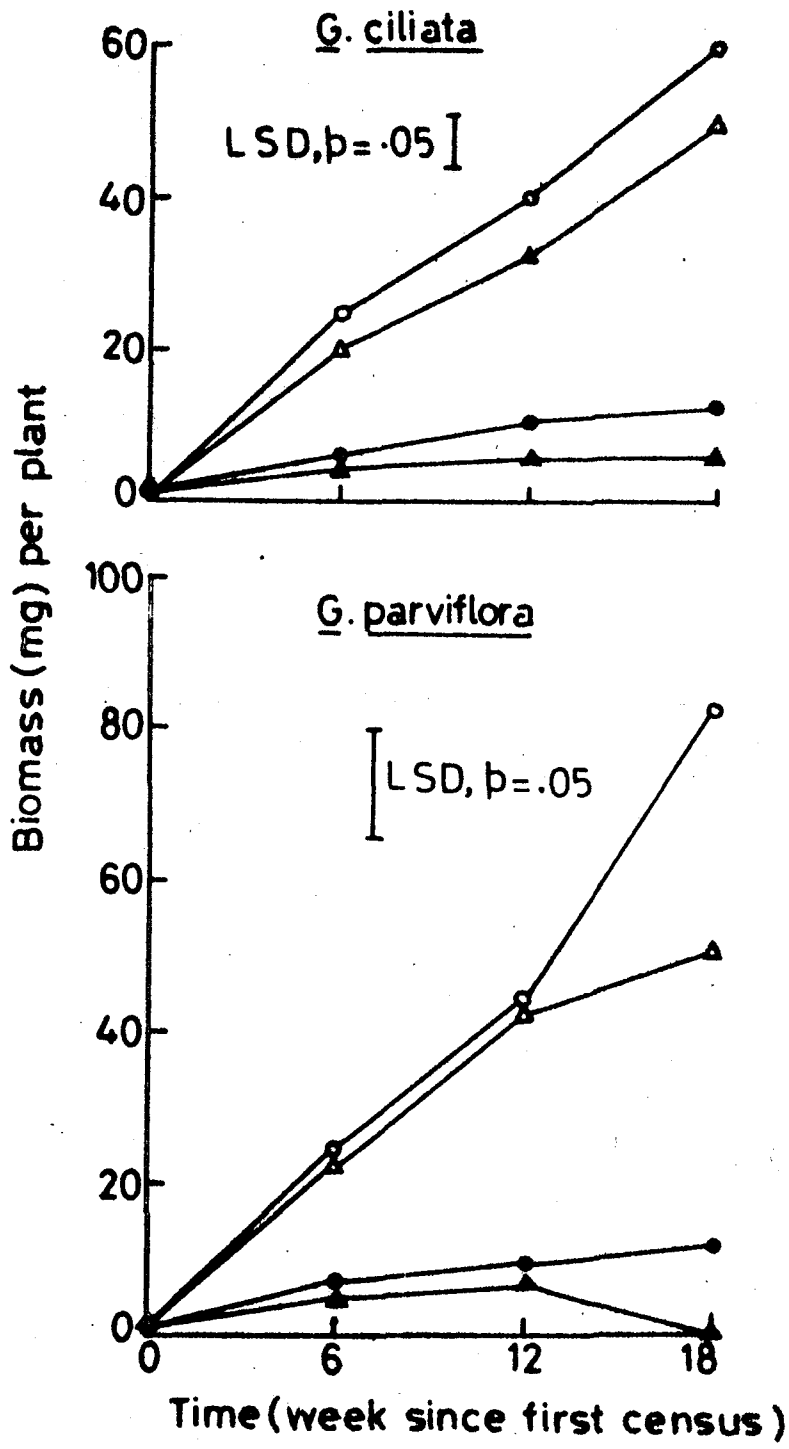


Fig. 4.3

Table 4.3: Reproductive behaviour of the two Galinsoga spp. as affected by the associated vegetation (\pm S.E.).

Nature of plant	Reproductive parameter	<u>G. ciliata</u>		<u>G. parviflora</u>	
		Without associates	With associates	Without associates	With associates
Seed born plant.	No. of capitula/ plant	22 \pm 1.8	0 \pm 0	34 \pm 2.6	0 \pm 0
	No. of seeds/ capitulum	17 \pm 1.3	0 \pm 0	23 \pm 0.9	0 \pm 0
	No. of seeds/ plant	365 \pm 22	0 \pm 0	775 \pm 29	0 \pm 0
Transplant	No. of capitula/ plant	28 \pm 2.6	2 \pm 1.0	35 \pm 2.8	0 \pm 0
	No. of seeds/ capitulum	17 \pm 2.1	17 \pm 2.9	22 \pm 3.1	0 \pm 0
	No. of seeds/ plant	638 \pm 152	331 \pm 15	770 \pm 84	0 \pm 0

DISCUSSION

The results indicate that the associated vegetation caused spectacular decrease in seed germination, survivorship and growth of the two Galinsoga spp. G. ciliata was, however, less affected as compared to G. parviflora.

The decrease in seed germination of the two weeds in presence of the associates may be attributed to lack of enough 'safe sites' (Harper, 1961) and/or production of some seed germination inhibitors by the associated vegetation. E. adenophorum and E. riparium which grow as the dominant associated species on the study plots, are known to have allelopathic effect on seed germination of the two weeds (Tripathi et al., 1981; Rai & Tripathi, 1982b).

None of the seed born seedlings of G. parviflora survived over the whole study period presumably due to their inability to cope with competition from the associated vegetation. However, some seedlings of G. ciliata could manage to survive but they also failed to show any increase in either vegetative or reproductive growth, thus indicating the 'resistance to inanition' as argued by Chippindale (1948). This feature may probably confer a great advantage on this weed to survive the competitive rigours. Relatively better survival of the transplants of the two weeds than the seed born seedlings, when grown with the associates, indicates the significance of age in minimising the competition from associated vegetation. Cavers & Harper (1967) too, have

reported the better survival of phytometers as compared to seed born seedlings of Rumex spp.

The reduction in leaf area per plant of the two weeds when grown with the associates (Table 4.4) seems to be an important factor contributing to the death of individuals. It appears that the plants failed to develop the minimum leaf area needed for their sustenance. Relatively lesser reduction in leaf area per plant of G. ciliata also suggests that it could make some growth under stressed conditions as well, which resulted into better survival of this species.

The yield and reproductive growth of the two species of Galinsoga were also greatly reduced due to presence of the associates. There was complete absence of flowering and fruiting in G. parviflora when grown with the associates. However, in G. ciliata some transplants produced seeds but in this species as well, the seed born seedlings did not flower. Transplant of G. ciliata thus appear to be better adapted to grow in competition with the associates than the seed born seedlings. The adverse effect of associates, especially grass species on vegetative and reproductive growth of some plant species has also been observed by Sagar & Harper (1961) and Dwivedi & Tripathi (1980). The associates that are already established and well grown intercept the incoming solar radiation to a great extent. Thus, it may be argued that individuals of G. ciliata, showing better survivorship and yield even in the presence of associated vegetation, are better adapted to poor light

Table 4.4: Periodic percentage reduction in various growth parameters of the two species of Galinsoga as affected by the associated vegetation.

Nature of Plant	Parameter	<u>G. ciliata</u>			<u>G. parviflora</u>		
		Weeks after first census			Weeks after first census		
		6	12	18	6	12	18
Seed born plant	Leaf area/plant	80	89	90	86	93	*
	Yield/plant	79	81	87	74	85	*
Transplant	Leaf area/plant	83	94	94	88	91	94
	Yield/plant	74	74	78	71	80	85

* The percentage reduction was infinity as all the plants died off.

conditions. G. parviflora, showing greater susceptibility to competition stress from the associates, prefers relatively open habitats. A comparison of the extent of reduction in growth of the two species reveals that G. parviflora is more sensitive to competition and shade caused by the associates. This seems to be one of the reasons for the smaller population size of G. parviflora in nature as compared to co-existing G. ciliata.

- b) Allelopathic effect of E. riparium on seed germination and growth of the two Galinsoga spp.

INTRODUCTION

The associated vegetation, besides competing for resources, also produce some toxic substances which affect the growth and development of the neighbouring plant species (Rovira, 1969; Whittaker & Feeny, 1971). Changes in community structure and species - dominance have also been attributed to allelopathy in several studies (Muller, 1969; Neill & Rice, 1971; Rice, 1974, 1979; Lodhi, 1976; Friedman et al., 1977; Hull & Muller, 1977; Gliessman, 1978; Parker & Muller, 1979; Ballester et al., 1979). However, the role of allelopathy in regulating the populations of weedy species has not been emphasized much.

Eupatorium riparium Regel, a perennial herb of family Asteraceae grows abundantly on wasteland and roadsides as one of the noxious weeds of ruderal habitats at higher altitude in Meghalaya. Its dominance in nature over other plant species has been attributed to allelopathy (Rai & Tripathi, 1982b). It was pointed out that certain plant species especially the two annual weeds, G. ciliata and G. parviflora which are sympatric with E. riparium exhibited better growth and more density in field populations where they do not come in close contact with the latter. This leads to the assumption that E. riparium has some regulatory effect on the populations of the two species of Galinsoga. Thus, a study was carried out to examine whether

and to what extent the Galinsoga populations are affected by the allelopathic effects of E. riparium.

MATERIALS AND METHODS

Effect of E. riparium extracts and leachates on seed germination and radicle and plumule growth of Galinsoga spp.

Fresh leaves and litter of E. riparium were collected from field populations in May 1980 and aqueous extracts of 1% and 5% concentrations were obtained by crushing 1 and 5g of the leaves and litter in 100 ml distilled water with a pestle and mortar and by filtering the crushed material through a muslin cloth. The leaf leachate was prepared by shaking mechanically 1 and 5g of fresh leaf with 100 ml distilled water for 2 h. The freshly collected fully ripened seeds of G. ciliata and G. parviflora were soaked in the leaf extracts/leachates of different concentrations for 24 h. The corresponding controls, with the seeds of the two species soaked in distilled water for the same period, were also maintained. Fifty soaked seeds of each of the two species were kept in Petri dishes on moist filter paper for germination, and for each treatment three replicates were maintained. All the Petri dishes were kept in a BOD incubator at $25 \pm 2^\circ\text{C}$. Seed germination was recorded over a 15-days period after which the seed germination practically ceased to occur. The effect of extracts and leachates was studied on radicle and plumule elongation over 96 h duration. The plumule and radicle elongation was averaged on the

basis of ten measurements.

Growth of *Galinsoga* spp. as affected by *E. riparium* extract and leachate: Four day old five seedlings of each of the *Galinsoga* spp., with fully expanded cotyledonary leaves were separately transplanted on 20 July 1980 in each of the 36 plastic pots (21 cm diam. with a basal hole for drainage) containing 4 kg sandy loam soil. The pots were separated in four lots for application of 1% and 5% extracts and leachates. There were three replicates and three harvests for each of the four treatments. The aqueous extracts/leachates were prepared as described in experiment 1. Three hundred ml of each extract/leachate was supplied to each pot of the respective treatments at 3 days interval from the date of transplantation. Nine control pots where 300 ml of distilled water was supplied, were kept for each test species. The harvests were taken after 5, 10 and 15 weeks from the date of transplantation to determine the leaf area and number of capitula and seeds per plant. The dry matter production was determined after drying the plant material in an oven at 70°C for 48 h.

Effect of litter extract and litter bed: Experimental design to evaluate the effect of the litter extract was similar to that of experiment 2. Litter bed was prepared in pots containing soil overlain with 15 g of litter powder of *E. riparium*. Four day old 5 seedlings were transplanted in each pot. Three pots per treatment were harvested after 15 weeks from the

transplantation date and the growth parameters like leaf area, seed output and biomass production were measured.

Effect of *E. riparium* on *Galinsoga* populations: Twenty pots were filled with sandy loam soil. Two plants of *E. riparium* each having four leaves were transplanted in each of the 10 pots in March 1981. The other set of 10 pots contained no plant (control). After 4 months of growth *E. riparium* plants were uprooted from the pot soil and were left to dry and decompose in the pots for one month, after which the undecomposed plant material was removed from the pots. Hundred seeds of each of the two test species were separately sown in the treated and control pots. Seeds were also sown in pots filled with soil from the natural habitats of *E. riparium*. The seed germination was recorded after 15 days from sowing while the observations on number of survivors and dry matter production were made after 95 days from sowing.

Effect of decomposing litter of *E. riparium* on *Galinsoga* spp.:

Fresh plant litter was collected from the soil surface densely infested with *E. riparium*. Toxicity was tested by incorporating the litter to the soil at the rate of 500 g m^{-2} which is equivalent to the quantity of litter present on per m^2 area in the field. Both species of *Galinsoga* are characterised by having more than one seedling cohorts emerging at different time period in nature (Usami, 1976) and so, the seedlings are likely to be affected by the litter in different stages of

decomposition. To simulate this, the litter was added to the pot soil before 2, 10 and 20 weeks from the start of experiment. Fifty seeds of each of the two test species were sown per pot in the treated soil. The corresponding controls, where no litter was added were also kept for comparison. Three replicates per treatment were maintained. Seed germination was recorded after 15 days from sowing date. After 95 days from sowing, number of survivors and dry matter yield was estimated.

Statistical treatment of the data: The LSD and SE values were calculated to find out whether the differences were significant due to the treatments.

RESULTS

The seed germination and radicle and plumule growth of both the test species were considerably inhibited by extracts and leachates of E. riparium (Table 4.5). The inhibitory action was correlated with the concentration of extracts/leachates. The two species responded differentially to aqueous extract; in case of G. ciliata the leaf extract caused relatively greater inhibition while in G. parviflora maximum inhibition was caused by the litter extract.

Although the growth of both test species was adversely affected by the application of leaf extract/leachate of E. riparium to the pot soil (Fig. 4.4), G. parviflora was affected more. The leaf area and number of capitula and seeds

Table 4.5: Seed germination and radicle and plumule growth inhibition (%) of G. ciliata and G. parviflora caused by leaf extract, leachate and litter extract of E. riparium.

Test species	Leaf extract		Leaf leachate		Litter extract		LSD from control p = 0.05	
	1%	5%	1%	5%	1%	5%		
<u>G. ciliata</u>	Seed germination	20.9	61.8	4.3	12.4	18.7	33.9	8.5
	Radicle growth	53.8	67.3	14.7	39.4	5.6	35.8	12.8
	Plumule growth	53.7	65.5	19.2	28.5	12.7	26.9	13.6
<u>G. parviflora</u>	Seed germination	16.1	33.5	6.9	18.5	20.3	38.9	9.4
	Radicle growth	1.2	34.1	19.0	29.7	12.3	48.3	10.7
	Plumule growth	21.3	31.1	6.9	21.5	22.6	43.8	12.6

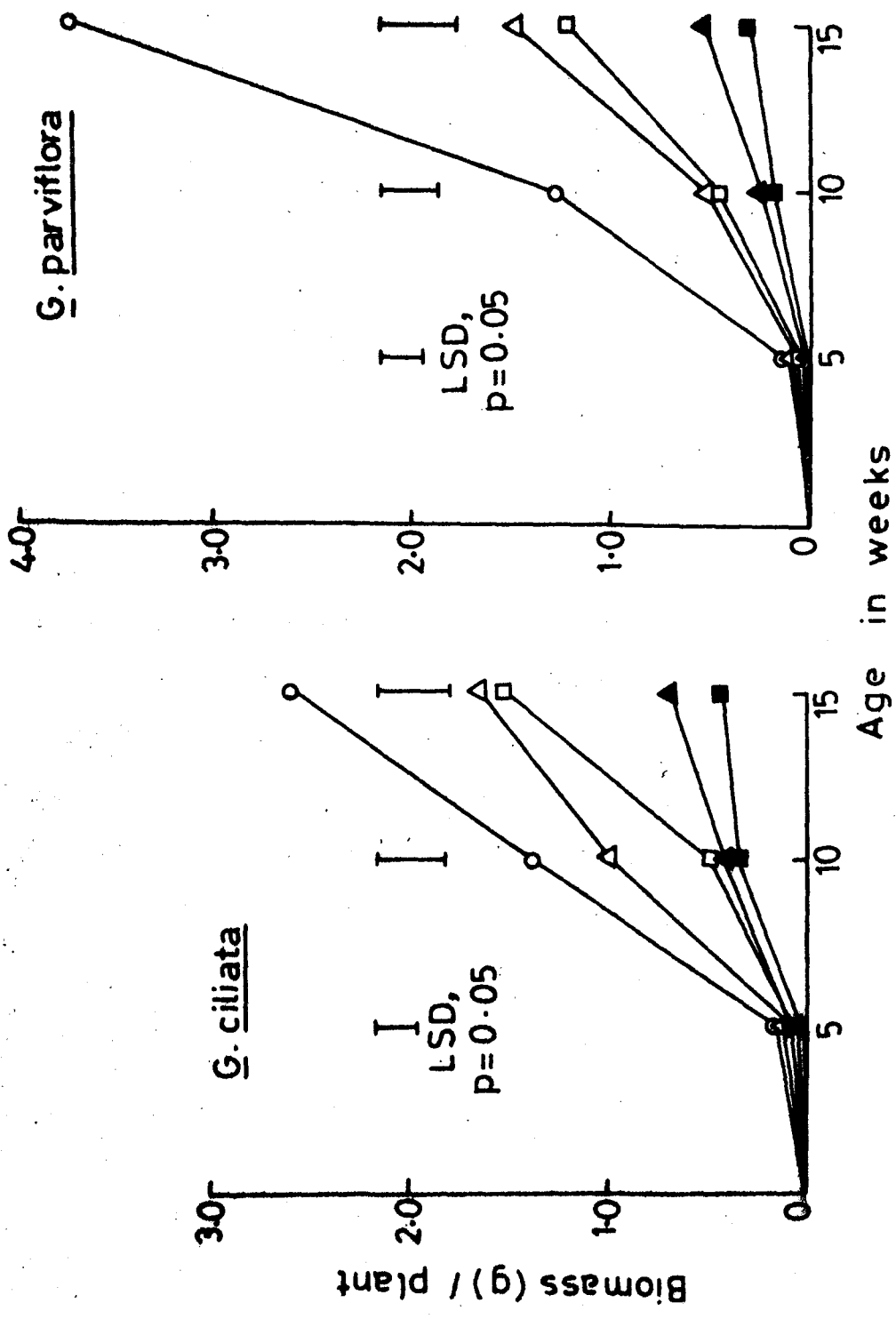


Fig 4.4

per plant of the two species were substantially reduced due to extract/leachate application (Table 4.6), but the number of seeds per capitulum remained unchanged. Similar reduction in growth performance of the test species was observed due to the litter extract application and amendment of soil with litter (Table 4.7). The leaf extract caused most inhibition, followed by the litter extract and leaf leachate (Table 4.8). The shoot growth of the test species was relatively more affected by the leaf extract and leaf leachate, while the root growth by the litter extract and litter bed.

Seed germination, survival and growth and reproductive allocation of both species were reduced when the plants were grown in soil collected from E. riparium stand (Table 4.9). G. parviflora was more adversely affected than G. ciliata.

The litter of E. riparium in different stages of decomposition in the soil caused reduction in seed germination, number of survivors and reproductive performance of both species (Table 4.10). The litter in early stage of decomposition inhibited the plant growth more adversely than in the later stage. The addition of the litter to the pot soil two weeks before seed sowing resulted into an increased shoot/root ratio, especially in G. ciliata.

DISCUSSION

Not only the germination of seeds of the Galinsoga spp. soaked with extracts and leachates of E. riparium was reduced

Table 4.6: Leaf area (cm²) and reproductive behaviour of G. ciliata and G. parviflora as affected by leaf extract and leachate of E. riparium (\pm S.E.).

	Control	Leaf extract		Leaf leachate	
	0%	1%	5%	1%	5%
<u>G. ciliata</u>					
Leaf area/plant	360.3 \pm 28.4	308.0 \pm 30.2	167.8 \pm 36.3	310.0 \pm 31.4	192.8 \pm 40.7
No. of capitula/plant	161.6 \pm 28.4	78.7 \pm 16.3	28.3 \pm 9.2	103.8 \pm 20.4	65.4 \pm 11.9
No. of seeds/capitulum	18.9 \pm 1.6	19.2 \pm 1.3	16.5 \pm 2.1	19.0 \pm 0.9	18.3 \pm 1.8
No. of seeds/plant	3055 \pm 601	1512 \pm 208	466 \pm 89	1972 \pm 401	1196 \pm 215
<u>G. parviflora</u>					
Leaf area/plant	406.6 \pm 80.3	226.0 \pm 72.9	133.7 \pm 10.8	228.0 \pm 70.3	135.0 \pm 12.1
No. of capitula/plant	99.3 \pm 13.3	45.0 \pm 12.1	11.3 \pm 4.3	59.9 \pm 14.3	16.4 \pm 2.4
No. of seeds/capitulum	25.0 \pm 2.7	24.0 \pm 1.2	24.2 \pm 1.6	26.1 \pm 2.1	23.9 \pm 1.6
No. of seeds/plant	2481 \pm 702	1080 \pm 103	272 \pm 48	1557 \pm 308	401 \pm \pm 82

Table 4.7: Leaf area (cm²), reproductive behaviour and dry weight (mg) of G. ciliata and G. parviflora as affected by litter extract and litter bed of E. riparium (+ S.E.)

	Control 0%	Litter 1%	extract 5%	Litter bed
<u>G. ciliata</u>				
Leaf area/plant	272.8±24.3	198.3±18.6	50.2±10.8	214.3±38.6
No. of capitula/plant	48.2±12.3	27.4± 4.6	10.4± 2.3	14.8± 4.1
No. of seeds/capitulum	17.4± 1.3	18.1± 1.6	17.9± 1.9	18.3± 2.1
No. of seeds/plant	838.± 212	496 ± 93	186 ± 26	271 ± 39
Dry weight/plant	812 ± 38	521 ± 23	255 ± 20	581 ± 28
<u>G. parviflora</u>				
Leaf area/plant	342.0±20.6	173.0±15.2	98.3±9.6	122.5±12.3
No. of capitula/plant	53.0±13.1	23.8± 5.0	12.8±4.3	9.6± 3.3
No. of seeds/capitulum	24.3± 1.6	24.7± 1.6	25.4±2.1	24.7± 2.1
No. of seeds/plant	1288 ± 210	588 ± 63	320 ± 49	237 ± 31
Dry weight/plant	1804 ± 41	752 ± 32	374 ± 17	338 ± 17

Table 4.8: The inhibitory effect (%) of leaf extract, leachate and litter extract and litter bed of E. riparium on leaf area, seed output and biomass of G. ciliata and G. parviflora.

	Leaf extract		Leaf leachate		Litter extract		Litter bed	LSD from control p = 0.05
	1%	5%	1%	5%	1%	5%		
<u>G. ciliata</u>								
Leaf area	14.4	53.5	13.9	46.5	27.3	81.6	21.5	22.2
Seed putput	50.5	84.7	35.5	60.8	40.8	77.8	67.6	37.3
Root biomass	25.3	58.0	13.5	40.2	50.0	77.0	62.5	30.1
Shoot biomass	44.0	80.0	30.5	59.0	39.2	70.0	34.5	35.2
<u>G. parviflora</u>								
Leaf area	44.5	67.1	44.0	66.8	49.4	71.3	64.2	44.7
Seed output	56.5	88.8	37.2	83.8	54.4	75.2	81.6	38.3
Root biomass	50.0	68.2	24.0	53.8	57.0	81.5	78.0	26.5
Shoot biomass	59.6	89.3	42.0	64.1	54.2	77.0	78.2	44.2

Table 4.9: Seed germination, survivorship, dry matter yield and reproductive allocation of G. ciliata and G. parviflora as affected by the growth of E. riparium.

Test species	Nature of pot soil	Seed germination (%)	Survivorship (%)	Yield/pot (g)	Reproductive allocation (%)
<u>G. ciliata</u>	Soil from natural habitat of <u>E. riparium</u>	80.0	47.8	4.2	10.7
	Soil from pots containing <u>E. riparium</u>	67.5	43.5	4.0	12.8
	Soil from pots devoid of <u>E. riparium</u>	86.3	58.7	5.2	13.7
	LSD, p = 0.05	18.6	5.5	1.0	3.9
<u>G. parviflora</u>	Soil from natural habitat of <u>E. riparium</u>	76.6	36.5	4.9	7.1
	Soil from pots containing <u>E. riparium</u>	72.6	39.1	4.9	8.8
	Soil from pots devoid of <u>E. riparium</u>	89.7	43.5	6.1	12.1
	LSD, p = 0.05	12.2	2.6	0.9	2.9

Table 4.10: Seed germination, survivorship, yield, shoot/root ratio and reproductive allocation of G. ciliata and G. parviflora as affected by decomposing litter of E. riparium.

Test species	Duration of litter decomposing in pot soil	Seed germination (%)	Survivorship (%)	Yield/pot (g)	Shoot/root ratio	Reproductive allocation (%)
<u>G. ciliata</u>	Control (No addition of litter)	75.6	81.1	2.7	11.6	9.6
	2 weeks	56.3	44.4	0.7	16.5	4.2
	10 weeks	65.6	59.4	1.8	12.5	6.8
	20 weeks	65.6	76.1	1.9	13.4	10.6
	LSD, p = 0.05	14.7	21.4	0.6	2.2	226
<u>G. parviflora</u>	Control (No addition of litter)	72.5	71.4	3.1	11.0	6.5
	2 weeks	50.7	42.8	0.9	13.5	3.9
	10 weeks	76.1	52.3	2.6	13.4	6.7
	20 weeks	68.2	61.3	2.3	12.6	6.6
	LSD, p = 0.05	16.3	19.2	0.5	2.4	1.0

but the growth of plumule and radicle emerging out of such seeds was also poor. Suppressed growth of the seedlings caused due to inhibitory action of E. riparium might render the already less competitive Galinsoga species still weaker to compete against E. riparium. Such an argument finds support from Lockerman & Putnam (1981). As a consequence, the competition and allelopathic effects of E. riparium on the Galinsoga spp. play a crucial role in population regulation of the latter. The shoot and root of the test species exhibit differential susceptibility to the plant extracts. For example, the root growth was much more affected by the litter extract, and soil amended with the litter of E. riparium as compared to shoot growth whereas the latter was relatively more adversely affected by the leaf extract. This is in agreement with the observation made by Tripathi et al. (1981).

Like other allelopathic plants (Naqui & Muller, 1975; Dirvi & Hussain, 1979; Hussain & Gadoon, 1981) E. riparium induced soil toxicity by releasing toxins through leaching during its active growth and during the decay of litter. As a result, the seed germination and growth of the Galinsoga species were reduced considerably when they were grown either in soil collected from natural habitats infested with E. riparium or in experimental pots containing the soil amended with the litter of E. riparium. This highlights the importance of allelopathy in population regulation of the species as has also been argued by Whittaker (1970). ~~Schubert~~ & Tisdale (1969) found that litter of Artemisia tridentata in early decomposition stage

retarded seed germination and seedling growth of several grasses but stimulated growth four weeks following germination, a behaviour observed in the present study too.

Interestingly enough, while the seed germination and growth of the test species were strongly inhibited by E. riparium in bio-assay tests, they do occur in nature as associates of E. riparium although in poor density (Rai & Tripathi, 1982b). This might be either due to buffering action of other plant species growing in the vicinity and/or due to difference between the concentrations of allelochemicals in nature and in the experiment. Heavy rainfall (> 3000 mm per year) received in Shillong might be having a great diluting effect on the allelochemicals produced by E. riparium. Thus, some plant species may presumably escape unaffected by allelochemicals produced by E. riparium and may not show the same extent of inhibition as observed in control conditions (Rice, 1974). del Moral & Cates (1971) and Stowe (1979) have also observed a weak correlation between field distribution of a plant species and the bio-assay tests pertaining to allelopathic effects.

The results highlight the importance of allelopathy as a potent factor of population regulation. The present bio-assay tests employed to assess the allelopathic effects of E. riparium suggests the presence of growth inhibitors which have controlling influence on seed germination and radicle and plumule growth of the two weeds. These chemical substances also regulate the weed seed populations by reducing the seed output

per plant. Thus the study provides an interesting example where a weed (E. riparium in the present instance) producing allelochemics contributes to the population regulation of the other two weed species.

- c) Effect of established populations of G. ciliata and G. parviflora on their late emerging seedling cohorts.

INTRODUCTION

Colonising species which propagate largely through seeds usually have many seedling cohorts emerging at different times of the year. The late emerging seedling cohorts are exposed to competition for the available resources from the earlier established cohorts of different ages. Thus it would be interesting to understand, in what way the earlier emerged seedling cohorts affect the survival and growth of the new recruits of its own species. The most common belief is that the individuals that are already established gain better access to the available resources as compared to those arriving later (Werner, 1978), but quantitative measurements are meagre. The two exotic weedy species of Galinsoga exhibited the occurrence of more than one seedling cohorts in nature. An attempt has, therefore, been made to study the effect of earlier emerged seedling cohorts representing different age groups of the two weeds on emergence, survival and growth of the late emerging seedling cohorts.

MATERIALS AND METHODS

In order to maintain seedling cohorts of different age, two days old 10 seedlings of G. ciliata and G. parviflora were separately transplanted on 9 April, 4 May and 27 May 1981 in

plastic pots of 21 cm diam. each containing 4 kg sandy loam soil. These seedling cohorts were of 50, 25 and 2 days on 27 May 1981. On each planting date 8 pots were maintained for either of the two species. Out of these pots, half were sown with seeds of each species on 27 May 1981 at the rate of 100 seeds per pot. A control set for each of the two species was maintained by sowing the seeds in pots where the seedlings were not planted. The treatments were as given below:

- i. G. ciliata seeds were sown in pots devoid of seedling or plant (control set).
- ii. G. ciliata seeds were sown in pots containing 2 days old G. ciliata plants.
- iii. G. ciliata seeds were sown in pots containing 2 days old G. parviflora plants.
- iv. G. ciliata seeds were sown in pots containing 25 days old G. ciliata plants.
- v. G. ciliata seeds were sown in pots containing 25 days old G. parviflora plants.
- vi. G. ciliata seeds were sown in pots containing 50 days old G. ciliata plants.
- vii. G. ciliata seeds were sown in pots containing 50 days old G. parviflora plants.

Similar treatments were maintained with G. parviflora seeds too. The experimental design consisted of 7 treatments x 2 species x 4 replicates, involving 56 pots which were randomised completely. All the pots were supplied with equal

amount of water and were kept in polythene roofed net house.

After 15 days of sowing the emerged seedlings were marked and their fate was followed till the flowering and seeding at about fortnightly intervals. The plants were harvested for growth measurement on August 25 and 26, 1981. The above-ground, belowground and total biomass of the two species were estimated after drying the plant material at 60°C in an oven for 72 h.

RESULTS

Seed germination:

Seed germination of the two weeds decreased considerably in the pots containing the earlier emerged seedling cohorts (Fig. 4.5). The seeds of Galinsoga spp. sown with the seedling cohorts of the other species of Galinsoga showed relatively greater reduction in seed germination.

Survivorship of the seedlings:

Total number of survivors of the two weeds decreased with the advancing age of the earlier cohorts and the decrease was more when one species grew with another species (Fig. 4.5). G. parviflora grown with 25 days old cohort of G. ciliata showed 80% mortality which was even more than that observed with 50 days old cohort. In general, G. ciliata exhibited better survival than G. parviflora.

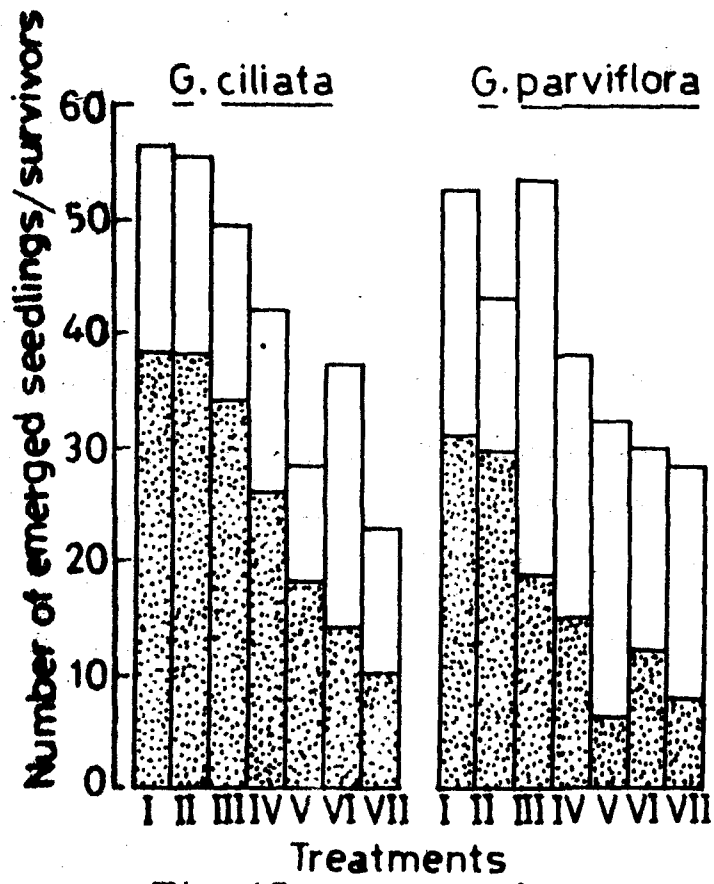


Fig. 45

The seedlings emerged from the sown seeds followed a similar pattern of mortality. The mortality was heavier during early stage of life and it decreased as the seedling population became older (Fig. 4.6). The seedlings of the two species responded to competition offered by the earlier established cohorts in different ways. As compared to the control, G. ciliata seedlings facing stress from the established cohorts exhibited relatively prolonged mortality that continued throughout the life whilst G. parviflora showed two fold increase in mortality during juvenile phase.

Leaf area:

The leaf area per pot of the two species decreased considerably with increase in age of the established cohorts (Fig. 4.7). The reduction in leaf area caused due to presence of the established cohorts was more conspicuous when one species was grown with another, the effect being more pronounced in G. parviflora which appears to be more sensitive to competition from the established cohorts.

Per plant leaf area of both species was also reduced substantially by competition from the established cohorts (Fig. 4.7). However, the extent of reduction was relatively less as compared to decrease in total leaf area per pot. G. parviflora exhibited relatively greater leaf area per plant than the other species although it was more susceptible to competition from the established cohorts. 25 days old G. ciliata cohort reduced the leaf area of G. parviflora by 58%, which was even more

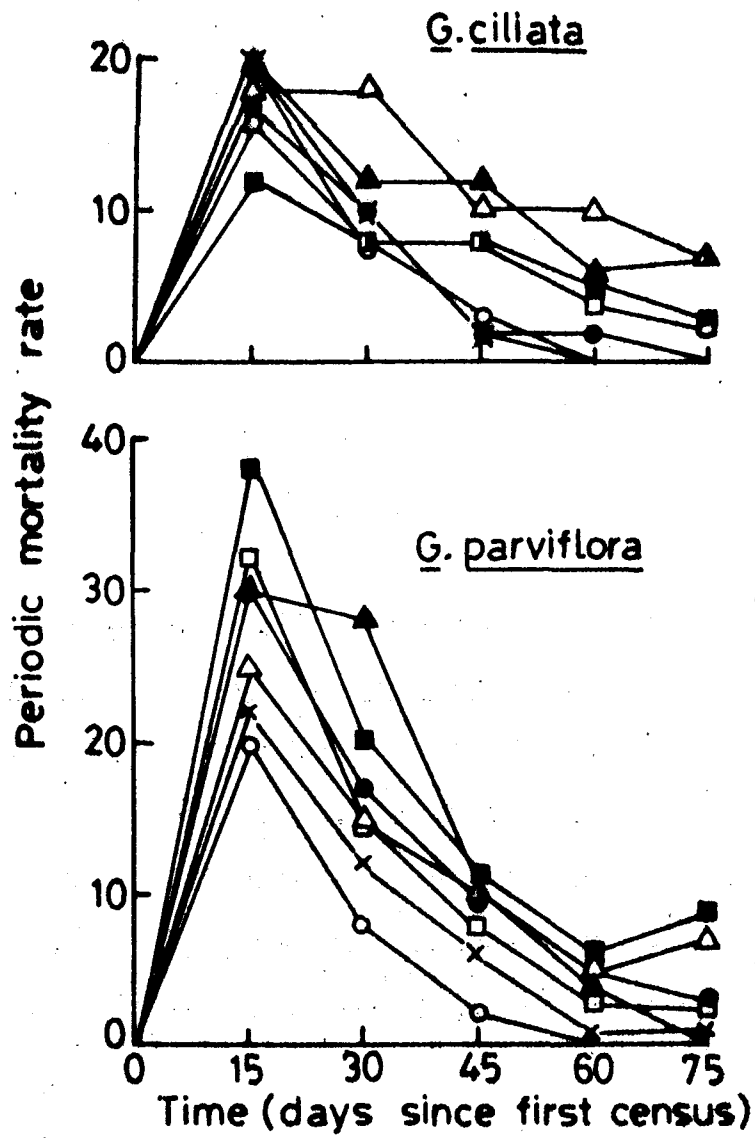


Fig. 4.6

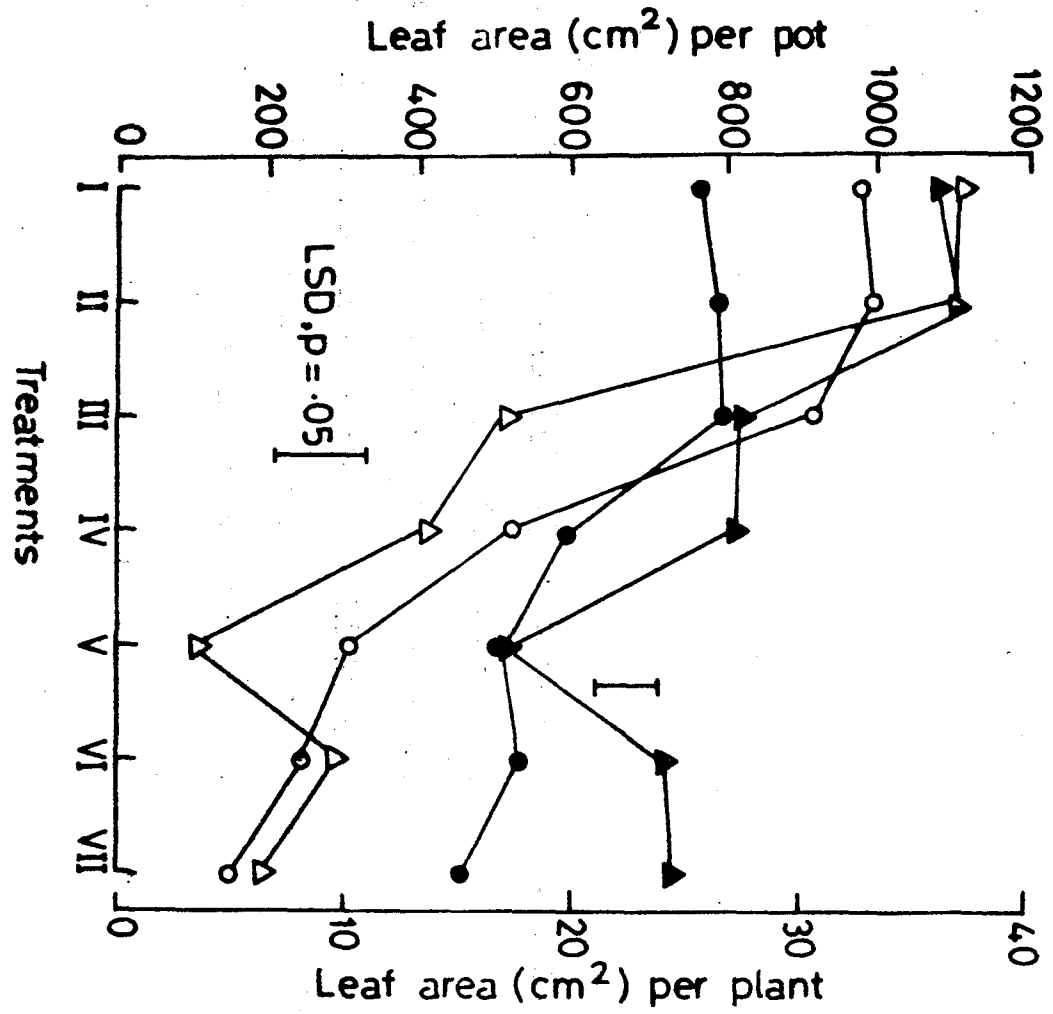


Fig. 4.7

than the reduction caused by the 50 days old cohort of the same species.

Biomass accumulation:

Per plant and per unit area yield of both species were **adversely** affected by their established cohorts and the effect was correlated with age of the established cohorts (Fig. 4.8). The two species responded differently to competition from the established cohorts; whereas the yield of G. ciliata was not reduced while growing with G. parviflora, the latter species showed 38% reduction in yield when grown with G. ciliata. Like other growth parameters, biomass of G. parviflora was also greatly suppressed by 25 days old G. ciliata cohort.

Reproductive growth:

Reproductive performance of the two weeds was also adversely affected by the growth of the established cohorts as indicated by the reduction in percentage of fertile plants and number of capitula and seed per plant (Table 4.11). The older the established cohorts, the more the reduction in reproductive growth caused by them. G. ciliata grown with established cohort of G. parviflora exhibited greater fertility and produced more capitula and seeds than when it was grown with its own established cohorts, whilst the reverse trend was observed in case of G. parviflora. G. parviflora grown with 25 days old cohorts of G. ciliata failed to flower, while growing with the two and fifty days/^{old}cohorts of the same species, G. parviflora

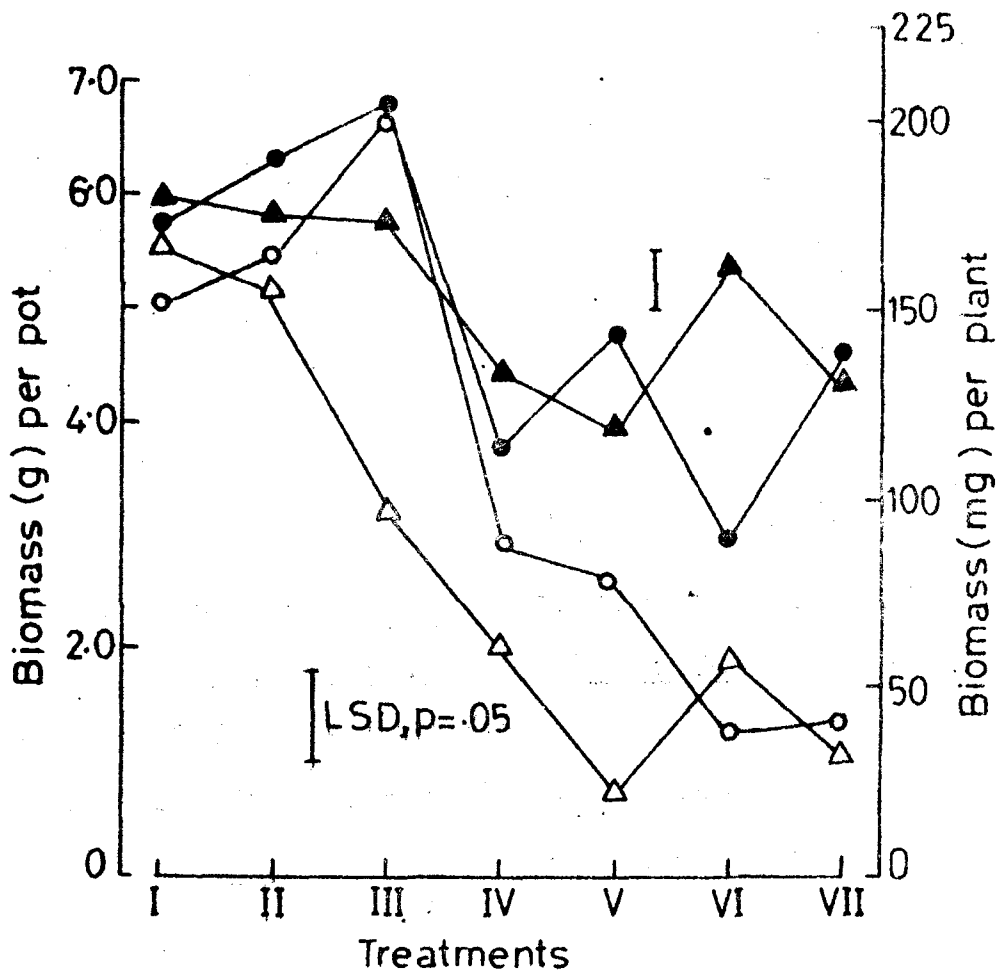


Fig. 4.8

Table 4.11: Reproductive growth of the two Galinsoga spp. when grown with their established plants of varying age (\pm S.E.)

Species	Parameter	Treatments*						
		I	II	III	IV	V	VI	VII
<u>G. ciliata</u>	Percentage of fertile plant	100 \pm 0	100 \pm 0	100 \pm 0	76.9 \pm 4.3	88.8 \pm 5.3	57.1 \pm 3.4	30.0 \pm 3.9
	No. of capitula/ plant	5.6 \pm 1.0	5.8 \pm 0.9	6.2 \pm 1.2	2.6 \pm 0.8	2.9 \pm 0.3	1.2 \pm 0.4	1.4 \pm 0.3
	No. of seeds/ capitulum	16.2 \pm 1.2	16.4 \pm 0.9	16.2 \pm 1.4	14.3 \pm 1.2	14.1 \pm 1.2	14.0 \pm 1.0	13.8 \pm 1.0
	No. of seeds/ plant	91 \pm 7.5	95 \pm 8	100 \pm 12	37 \pm 2	41 \pm 4	17 \pm 4	19 \pm 3
<u>G. parviflora</u>	Percentage of fertile plant	100 \pm 0	100 \pm 0	100 \pm 0	40.0 \pm 3.8	0 \pm 0	50.0 \pm 4.3	25.0 \pm 3.8
	No. of capitula/ plant	3.9 \pm 1.0	4.2 \pm 1.3	3.5 \pm 1.2	1.8 \pm 1.0	0 \pm 0	0.9 \pm 0.3	0.4 \pm 0.2
	No. of seeds/ capitulum	21.0 \pm 1.0	22.2 \pm 1.6	22.4 \pm 1.0	20.0 \pm 1.2	0 \pm 0	18.2 \pm 1.4	19.6 \pm 2.1
	No. of seeds/ plant	82 \pm 7.5	93. \pm 8.2	78 \pm 4.9	36 \pm 3.8	0 \pm 0	16 \pm 2	8 \pm 2

* The treatments I - VII are described under "Materials and Methods".

did show some flowering.

Percentage reproductive allocation of biomass in the two weeds also decreased in response to competition from the established cohorts (Table 4.12). However, the reduction was more in G. parviflora than G. ciliata. On contrary to G. ciliata, the reproductive allocation in G. parviflora was more adversely affected by the established cohorts of G. ciliata than by its own established cohorts. The reduction in reproductive allocation was correlated with the age of the established cohorts. However, 25 days old cohort of G. ciliata caused complete suppression of flowering while competition from the 50 days old cohort of G. ciliata did not stop flowering in G. parviflora completely.

DISCUSSION

The reduced seed germination of the two species, in pots where the established cohorts were present, may be attributed to non-availability of enough 'safe-sites.' Further, the shade cast by the older cohorts may cause death of newly recruited seedlings soon after their emergence before they became big enough to be recorded. This is in conformity with the findings of Tamm (1956) and Singh (1980), who reported poor germination and seedling establishment in established communities.

The survival and growth of the seedlings of G. ciliata and G. parviflora was greatly reduced due to competition from the established cohorts, and the reduction was often correlated

Table 4.12: Percentage biomass allocation to reproductive parts of the two Galinsoga spp. when grown with their established plants of varying age.

Species	Treatments*						
	I	II	III	IV	V	VI	VII
<u>G. ciliata</u>	14.8	15.3	17.1	7.1	8.9	3.1	3.2
<u>G. parviflora</u>	10.1	10.3	8.3	3.1	0	2.2	1.0

* The treatments I - VII are described under "Materials and Methods".

with the age of the cohorts. The newly born seedlings failed to establish due to severe competition offered by the older cohorts. Both species responded through mortality and plasticity. The increase in mortality due to competition from the established cohorts appears to have been adjusted by the two weeds in two different ways; in G. ciliata by prolongation of mortality risk throughout the life, whilst in G. parviflora by showing quite heavy mortality during early stage of life. The seedlings of one species showed higher mortality when it was allowed to grow with the cohorts of other species indicating the greater mortal response of the seedlings under interspecific competition. The results are in conformity with the observations of Friedman (1971) and Yadav & Tripathi (1982) on other plant species. The cohorts of G. ciliata, however, exercised more adverse effect compared to G. parviflora cohorts. Seedlings of G. parviflora experienced maximum mortality when grown with 25 days old cohort of G. ciliata, which was even larger than that observed with 50 days old cohort. This behaviour may probably be attributed to fluctuation in degree of interference from the active phase (represented by 25 days old cohort) and passive growth phase (represented by 50 days old cohort) of G. ciliata.

The growth of seedlings of the two species was generally retarded as shown in Table 4.13, due to the established cohorts. Established cohort of G. ciliata suppressed the growth of its own seedlings as well as the seedlings of G. parviflora, showing that G. ciliata plays more important role in population

Table 4.13: Percentage reduction (-) or increase (+) in various growth parameters of the two Galinsoga spp. when grown with their established plants of varying age.

Species	Parameter	Treatments*					
		II	III	IV	V	VI	VII
<u>G. ciliata</u>	Leaf area/plant	+3.2	+5.2	-21.9	-32.9	-30.0	-40.4
	Biomass/plant	+7.1	+31.2	-26.0	-6.5	-41.6	-9.8
	Seed output/plant	+4.9	+10.7	-59.0	-54.9	-81.5	-78.7
<u>G. parviflora</u>	Leaf area/plant	+2.8	-24.1	-24.4	-52.7	-33.0	-34.2
	Biomass/plant	-2.3	-2.8	-25.3	-33.7	-9.6	-27.0
	Seed output/plant	+13.8	-4.3	-56.0	-100.0	-80.0	-90.4

* The treatments II— VII are described under "Materials and Methods".

regulation of these two weeds. The greater regulatory influence of G. ciliata may be attributed to its frequent branching and faster growth which cast more shade in pots. Thus, the availability of light to the newly born seedlings may be curtailed to cause suppression in growth. The argument finds support from Andel & Rozema (1974) who observed keen competition for water between seedlings and adults of Chamaenerion angustifolium, as a consequence of which nutrient uptake by the seedlings was adversely affected. Relatively lesser reduction in seedling growth of both the species caused by G. parviflora cohorts may be attributed to their erect habit and open canopy. Seedlings of G. ciliata exhibited better growth than those of G. parviflora in all the treatments, showing that the latter species is more susceptible to competition from the established cohorts of either species. This also indicates that the two weeds have differential demand for light to sustain them.

The adverse effect of the established cohort on reproductive growth of the two weeds is also apparent from the results. The reproductive allocation in G. ciliata was not reduced to that extent as in G. parviflora suggesting that the former species is relatively better adapted to competitive situations than the latter. In general, the reduction in reproductive performance of both weeds was a function of the age of the established cohorts. However, G. parviflora grown with 25 days old cohort of G. ciliata showed nil fertility and the survivors remained in the state of 'resistance to inanition'

a phenomenon described by Chippindale (1948), whereas some flowering took place when it grew with 50 days old cohort of G. ciliata.

The experimental results suggest that G. ciliata might exercise strong regulatory influence not only on the newly recruited seedling cohorts of G. parviflora but also on its own seedling population, both through increased death and plastic reduction in seed production of the surviving plants. However, in nature where the species diversity is more, some other associated species might also be suppressing the growth of G. ciliata rendering it weaker and so, the regulatory influence of this weed on G. parviflora as revealed in the present experiment could be assumed to be of lesser consequence.

CHAPTER V

Effect of sowing density, sowing pattern and soil moisture
and texture on population regulation of G. ciliata and
G. parviflora

INTRODUCTION

Annual or ephemeral species reproducing solely by seeds where the individual plants may be easily defined served as ideal organisms for population studies (Harper, 1977). The reproductive output of such species can also be exactly assessed in the varied environments which prevail in the field. Seed output from a population depends on the seed population in the soil and the germination and subsequent fate of individuals at various stages of the life cycle.

The population response of certain species to gradients of environmental factors including moisture has been studied in nature (Redmann, 1975) and in experimental conditions (Muller-Dombois & Sims, 1966). The effect of density and moisture levels on plant populations has been emphasized by various workers (Hickman, 1975; Snell & Burch, 1975; Foulds, 1978; Rahman & Rutter, 1980). Besides these, the pattern of sowing also affects the plant populations as reported by Linhart (1976). Thus the present study aims to examine the population response of the two annual weeds, G. ciliata and G. parviflora, in relation to population density, pattern of sowing and soil moisture and texture.

MATERIALS AND METHODS

A large number of mature seeds (cypselae) of each of the two weeds was collected from the natural populations growing on the campus of the School of Life Sciences, North-Eastern Hill

University, Shillong and stored in paper bags.) (The viability of seeds as tested by terazolium solution (Misra, 1968) was 96% in G. ciliata and 100% in G. parviflora. (Seeds of uniform size (weight per thousand seeds was 225 ± 2.2 mg in G. ciliata and 267 ± 2.6 mg in G. parviflora) were sown in plastic pots (21 cm inner diameter and 19 cm depth with a hole on the bottom) filled with two types of soil viz., clay loam (clay 34%, silt 20% and sand 46%) and sandy loam (clay 18%, silt 10% and sand 72%). The nitrogen, organic matter and pH of the two soil types are given in Table 5.1. Nitrogen was estimated by the Kjeldahl method

Table 5.1: Initial nitrogen and organic matter content (%) and pH of the two soil types (means \pm S.E.).

<u>Soil type</u>	<u>Nitrogen</u>	<u>Organic matter</u>	<u>pH</u>
Clay loam soil	$0.2 \pm .01$	3.5 ± 0.2	6.2 ± 0.1
Sandy loam soil	$0.3 \pm .01$	3.3 ± 0.1	5.7 ± 0.2

(Jackson, 1962) and organic matter by rapid titration method (Walkley & Black, 1934).) 10, 30, 90 and 270 seeds of a given species were sown in each pot on April 13 and 14, 1980. These sowing densities are equivalent to 300, 900, and 2700 and 8100 seeds/m². In order to see the effect of sowing pattern, the seeds were either sown in scattered but regular fashion or they were clumped in groups of 10 seeds with the help of appropriately drilled paper masks. (After seed sowing, the soil was moistened by supplying each pot with 300 ml of tap water. Subsequently, two moisture regimes (high and low) were maintained

throughout the experiment by watering the pots daily and at ten days interval. The experimental design consisted of 2 species x 4 seed sowing densities x 2 sowing patterns x 2 soil textures x 2 moisture regimes x 3 replicates, thus involving 192 pots. The pots were completely randomised and kept in an unheated and polythene roofed greenhouse (range of temperature, 16-38°C; mid day light intensity, c.28.5 x 10³ lux). In addition 4 pots, for each of the two moisture regimes, were kept as controls to estimate the germinable background buried seed populations of the two weeds in the soil used in the experiment.

Seedling emergence in each pot was observed on every fifth day upto May 9, 1980 i.e. for 25 days from the date of sowing after which the seed germination practically ceased to occur. The number of survivors and fertile plants per pot, and number of capitula and seeds per reproducing plant and per unit area were estimated in August 1980 after 17 weeks from the start of experiment when a majority of the reproducing plants had matured and completed seeding. After recording the above observations, the plants were excavated whole, washed thoroughly to remove the soil particles adhering to the roots, and oven dried at 80°C for 72 h and weighed for biomass estimation.

Analysis of variance and t-test were used, wherever necessary, to test the statistical significance of the results. The pattern of sowing significantly affected only seed germination and plant survival. Consequently, for all the other

parameters presented the data for sowing pattern have been pooled.

RESULTS

Seed germination and plant survival

The seedling emergence in control pots was negligible (<1 per pot). Seed germination showed a negative correlation with sowing density on both types of soil and with moisture regimes (Fig. 5.1). Both the species showed significantly ($p < 0.05$) enhanced seed germination due to clumping of sown seeds in almost all the treatments except in the case of G. parviflora seeds sown in clay loam soil at high moisture level (Fig. 5.1). Although seed germination in both the weeds was better in the sandy loam soil, only for G. parviflora was this soil effect significant. Of the other treatments moisture stress caused significant ($p < 0.05$) reduction in seed germination of G. ciliata in clay loam soil. G. parviflora also showed a similar response but only at high sowing density (Fig. 5.1).

G. ciliata showed better survival than G. parviflora in almost all the treatments although significant differences ($p < 0.05$) were observed only at low sowing density in the sandy loam soil (Fig. 5.2). G. parviflora, however, showed better survival in clay loam soil. Moisture stress and increased seedling density caused increased mortality in both the species (Fig. 5.2). Mortality was also related to pattern of sowing. In general, the seedling survival of G. ciliata was better

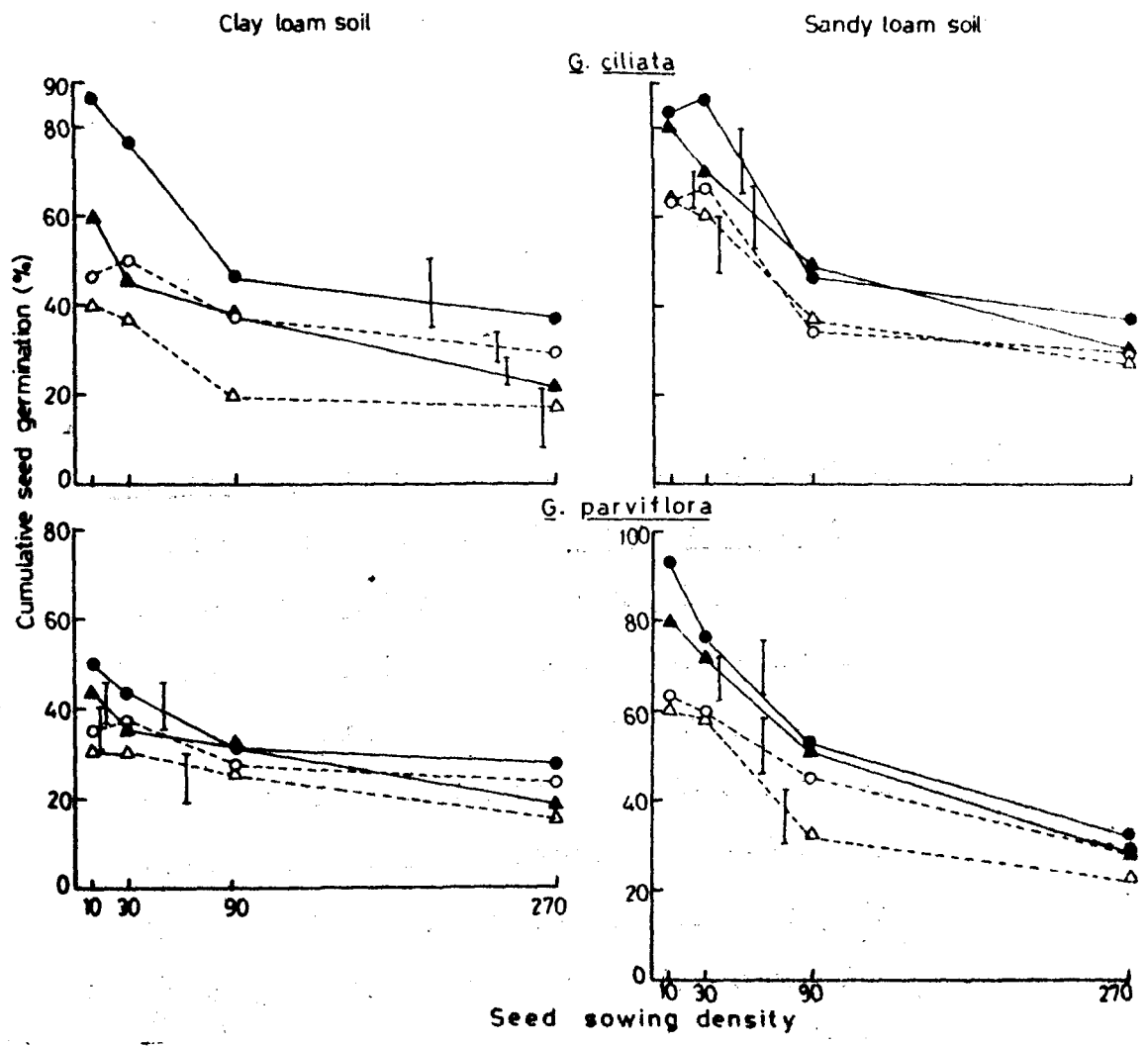


Fig. 5.1

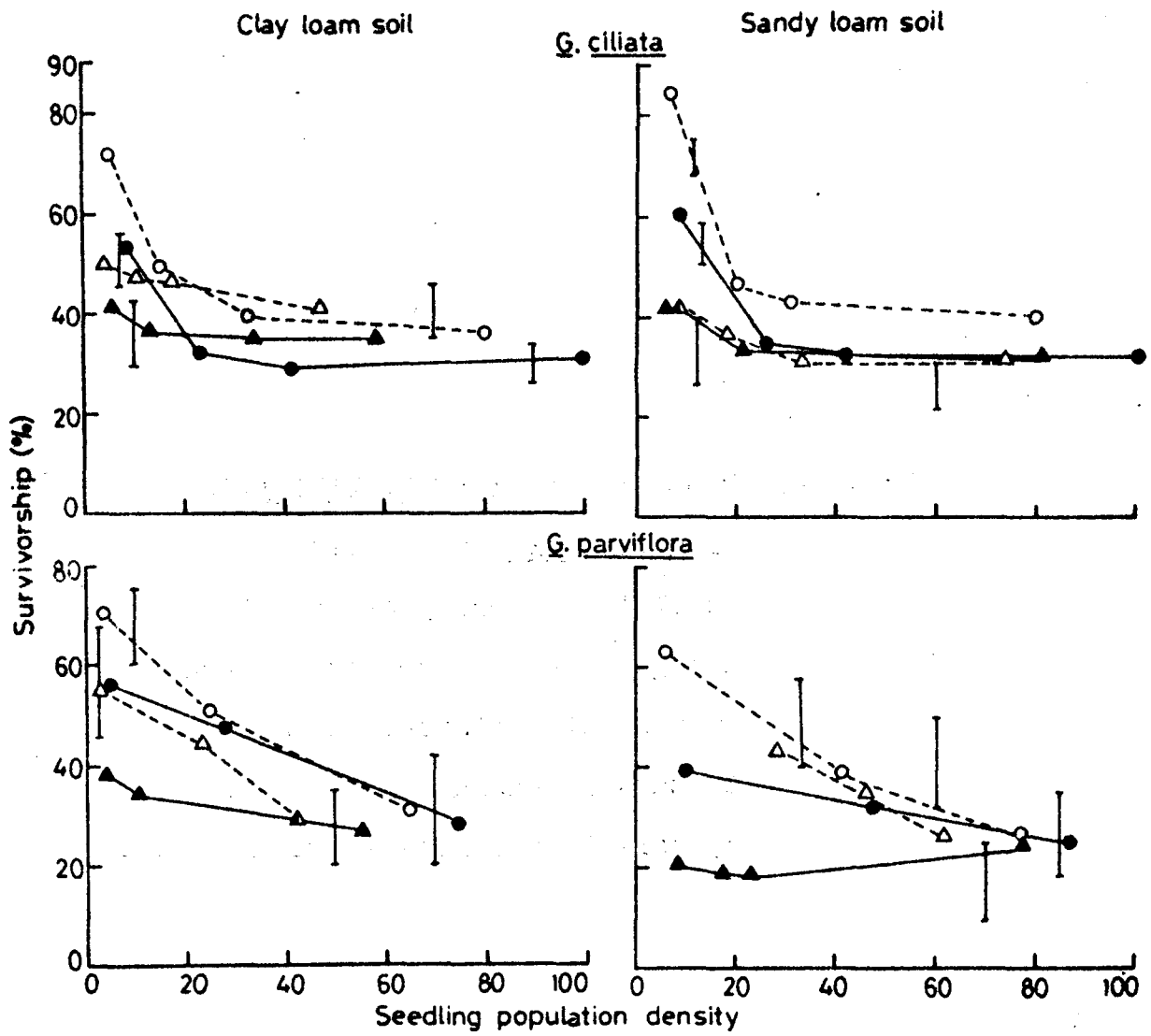


Fig 5-2

where the seeds were sown in scattered fashion ($p < 0.05$) with the exception in sandy loam soil at low moisture level (Fig. 5.2) but in G. parviflora this effect of scattering was observed only at low sowing density.

Growth and Phenology:

In both species plants in the high moisture regime were taller and reached maturity earlier than plants grown in the low moisture regime. At low sowing density (10 seeds/pot) and high moisture regime, plants grown in sandy loam soil showed better growth. Flowering in both species took place earlier at high moisture level; on average G. ciliata flowered 32 days and G. parviflora 8 days earlier. However, there was no significant effect of sowing density on flowering time of the two weeds.

Reproduction by survivors:

Most of the surviving plants at low sowing density (10 seeds/pot) reached maturity and produced seeds (96% in G. ciliata and up to 80% in G. parviflora). But as the population density increased the fertility percentage decreased (Fig. 5.3). At low moisture regime, a significant ($p < 0.05$) reduction in fertility was observed (Fig. 5.3). The soil texture had no significant effect on reproduction but in the low moisture regime both weeds tended to show greater fertility when grown in the sandy loam soil.

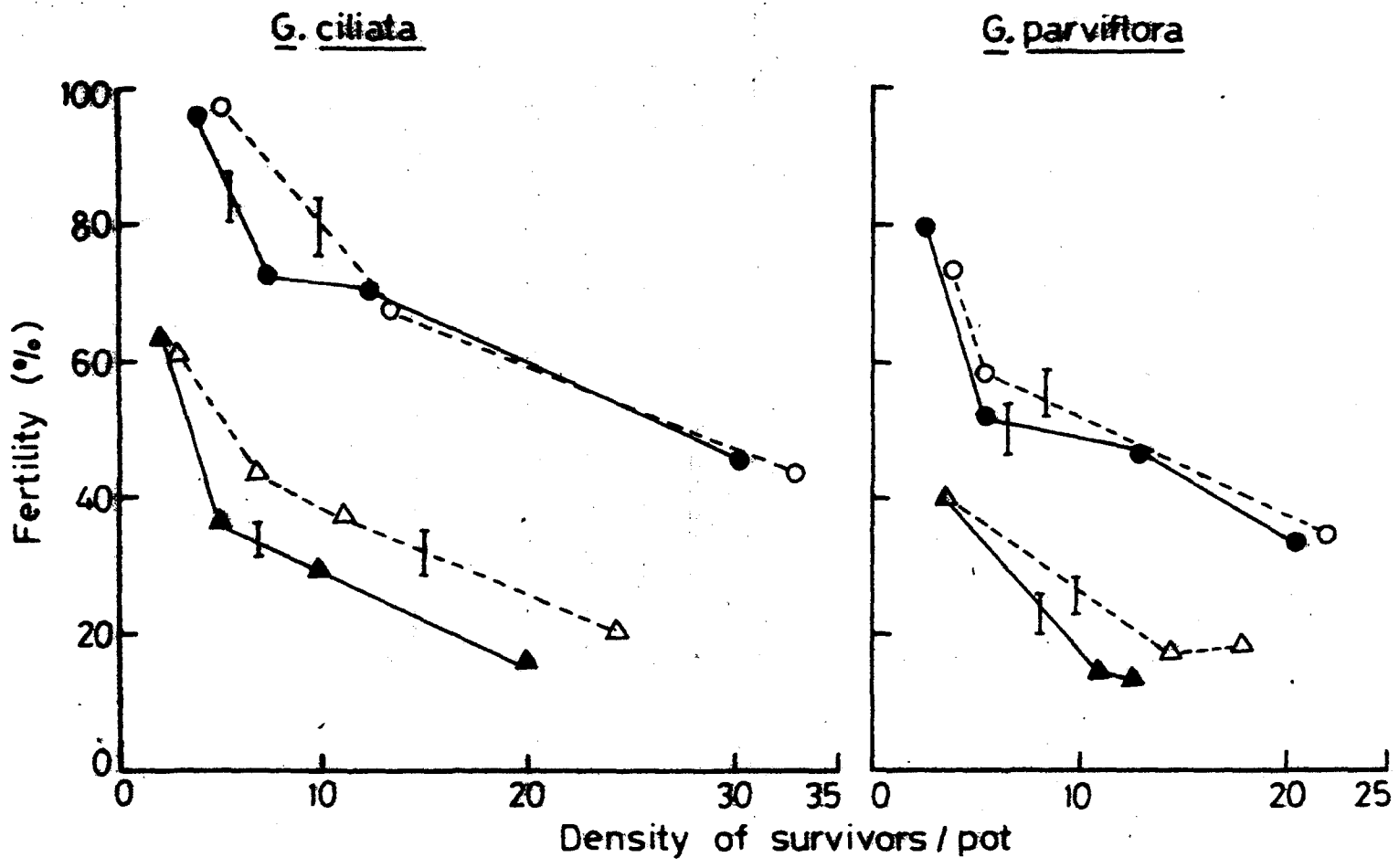


Fig. 5.3



Capitula production:

Number of capitula/pot increased with increase in density but at high densities (beyond 30 seeds/pot in G. parviflora and 90 seeds/pot in G. ciliata) (the value declined (Fig. 5.4). In moisture stressed situations, the production of capitula was substantially reduced and the variation due to increase in density was almost negligible. G. ciliata produced significantly greater ($p < 0.05$) numbers of capitula than G. parviflora. In general, the production of capitula in both species was higher in sandy loam soil than in clay loam (Fig. 5.4) but the differences were significant ($p < 0.01$) only in the case of G. parviflora at high moisture level.

Average number of capitula per reproducing individual in both species decreased with sowing density and moisture stress (Table 5.2). At high moisture level G. parviflora produced a significantly ($p < 0.05$) greater number of capitula in sandy loam soil than in clay loam but at low moisture level the differences due to texture were small. In G. ciliata, however, soil texture had no significant effect.

Seed production:

Total seed output per pot increased with sowing density and moisture level in both species (Fig. 5.5) but decreased at high densities. The increase in seed output with sowing density

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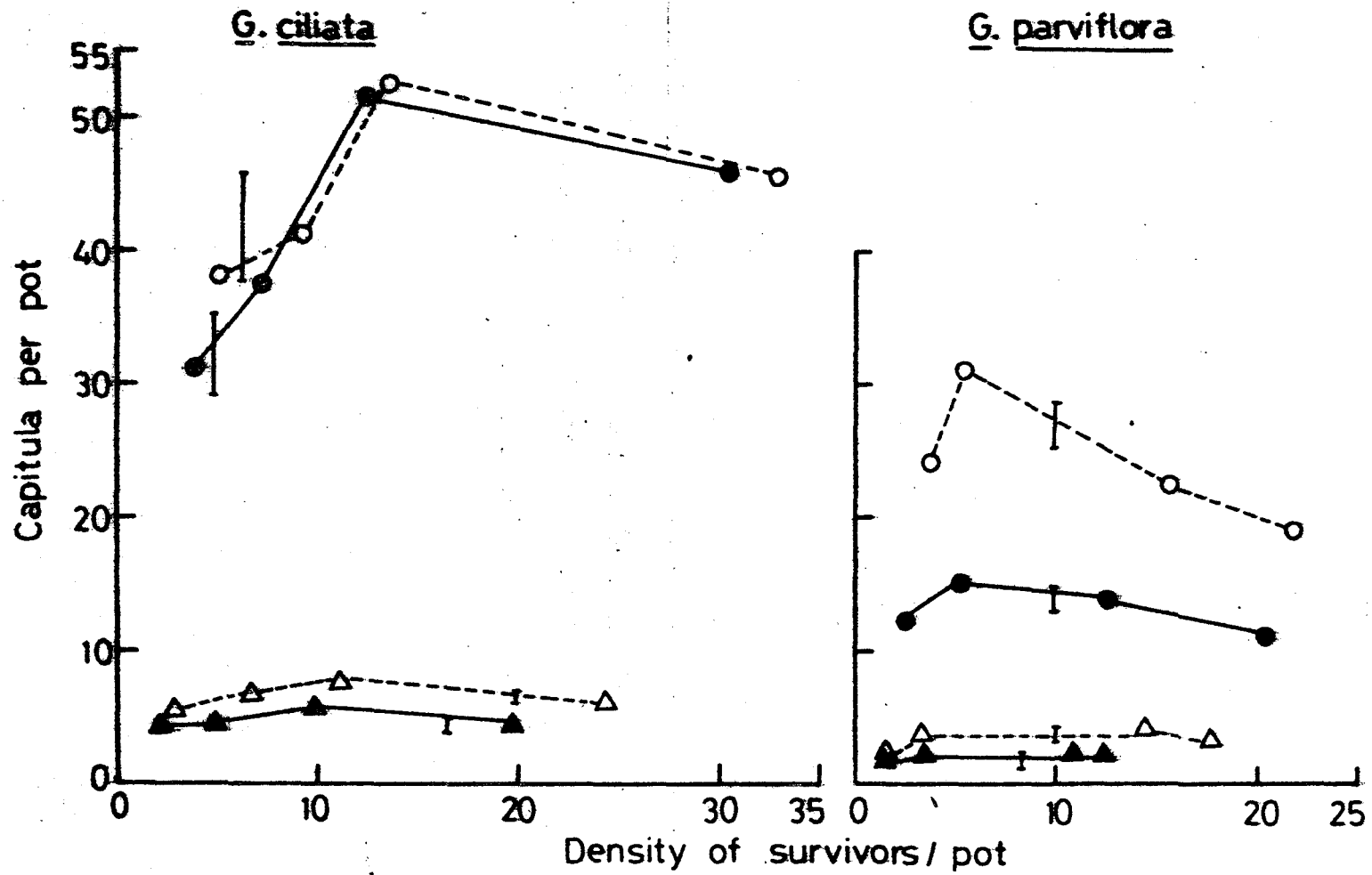


Fig. 5-4

Table 5.2: Mean capitula per reproducing plant of G. ciliata and G. parviflora grown from different sowing densities at two soil moisture regimes and textures.

Species	Moisture regime	Clay loam soil				Mean \pm S.E.	Sandy loam soil				Mean \pm S.E.
		Sowing densities per pot					Sowing densities per pot				
		10	30	90	270		10	30	90	270	
<u>G. ciliata</u>	High	8.4	7.0	5.9	3.4	6.2 \pm 1.1	7.6	6.9	5.8	3.1	5.9 \pm 1.0
	Low	3.0	2.4	2.1	1.5	2.3 \pm 0.3	2.9	2.2	1.8	1.5	2.1 \pm 0.3
<u>G. parviflora</u>	High	5.9	5.4	2.3	1.6	3.8 \pm 1.1	8.7	9.9	3.8	2.5	6.2 \pm 1.8
	Low	2.5	1.6	1.4	1.3	1.7 \pm 0.3	3.2	2.7	1.6	1.1	2.1 \pm 0.5
	Mean \pm S.E.	4.9 \pm 1.4	4.1 \pm 1.3	2.9 \pm 1.0	1.9 \pm 0.5		5.6 \pm 1.5	5.4 \pm 1.8	3.2 \pm 1.0	2.0 \pm 0.4	

Source of variation	Probability	Source of variation	Probability
Species	Not significant	Soil texture	Not significant
Moisture regime	< 0.01	Density	Not significant
Soil texture	Not significant	Soil texture x density	Not significant
Species x moisture regime	Not significant	Error	Not significant
Moisture regime x soil texture	Not significant		
Species x soil texture	Not significant		
Species x moisture regime x soil texture	Not significant		

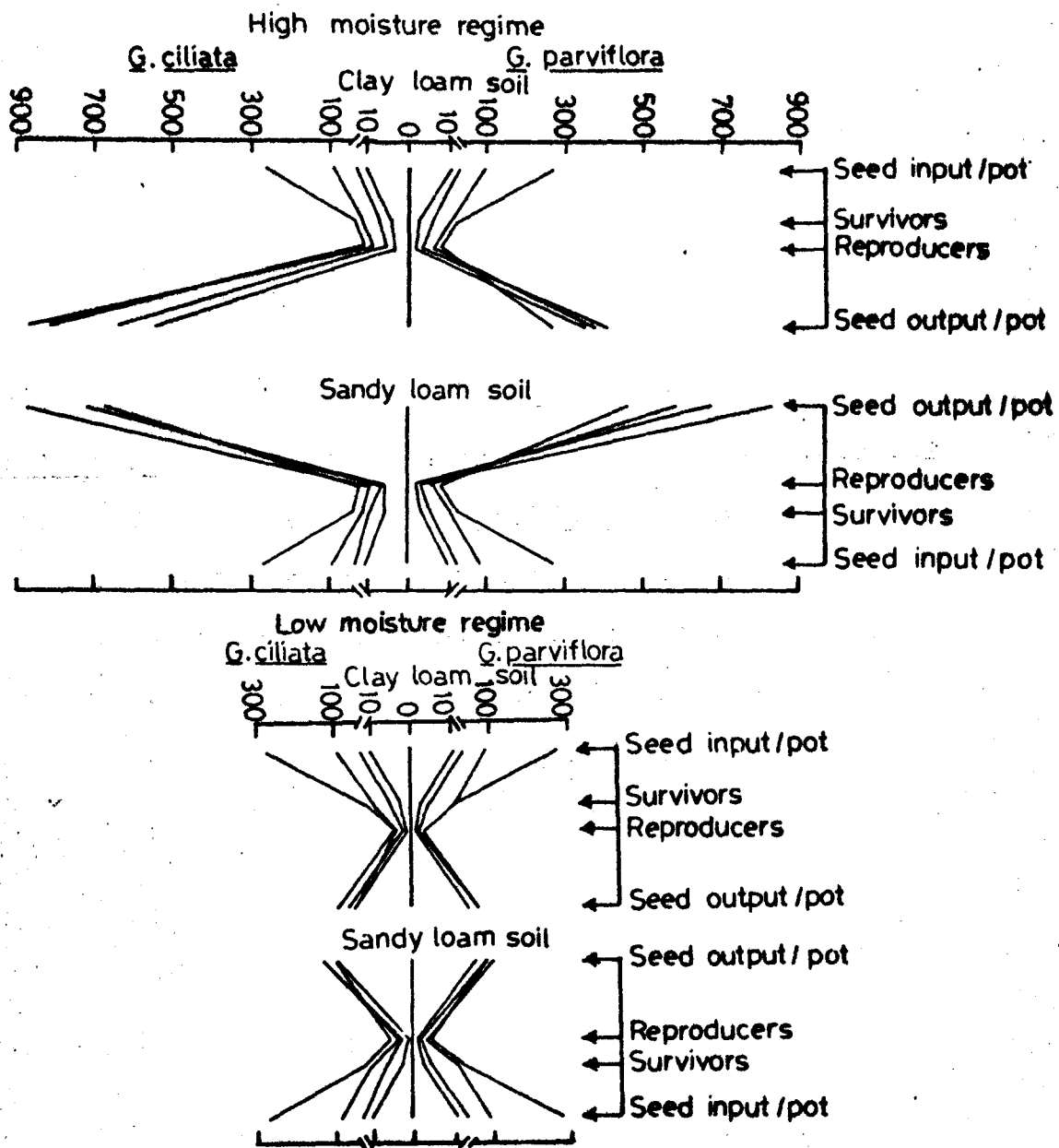


Fig. 5-5

up to the optimum level was more marked at high moisture level. Seed production over the four sowing densities was also influenced by the soil moisture level. G. ciliata produced maximum seeds at a sowing density of 90 seeds/pot while in G. parviflora the maxima were attained at a sowing density of 30 seeds per pot at the high moisture regime, and at 90 seeds/pot under the low moisture regime. In general, both the weeds tended to produce more seeds when grown in sandy loam soil but only G. parviflora showed a significant difference ($p < 0.01$) although only at the high moisture level (Fig. 5.5).

Seed output per reproducing plant of G. parviflora showed greater variation with population densities and moisture levels than G. ciliata (Fig. 5.6). Seed production/plant of G. parviflora increased significantly ($p < 0.05$) in sandy loam soil over that in the clay loam at high moisture level. With increase in population density, there was a marked decrease in number of seeds per reproducing plant in both species.

The mean number of seeds per capitulum in both species did not show any significant variation with sowing density, soil texture or moisture level (Table 5.3). However, G. parviflora showed a decreasing trend in number of seeds per capitulum with increase in population density.

Moisture stress and increasing sowing density caused significant ($p < 0.01$) reduction in seed output/input ratio in

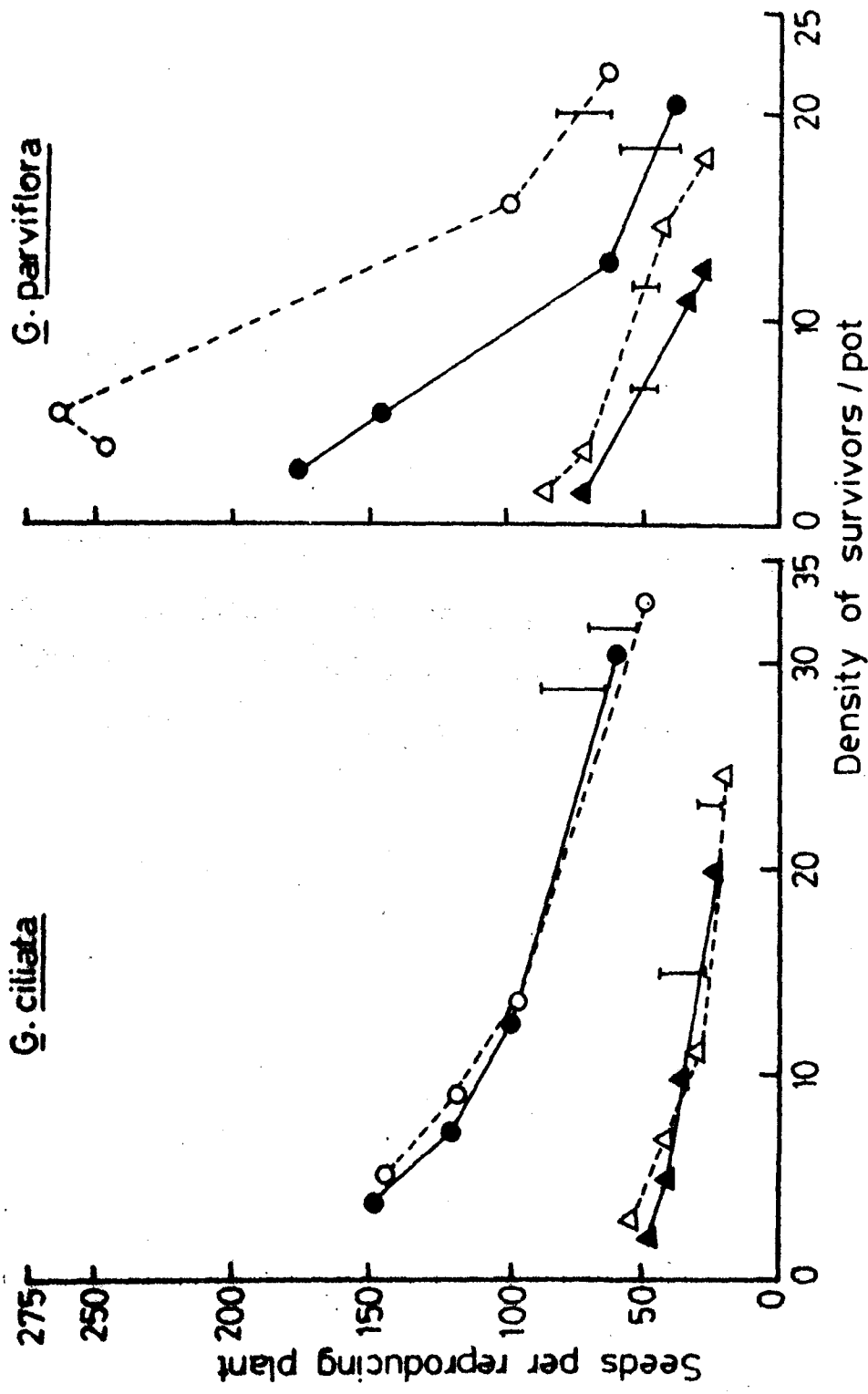


Fig. 5.6

Table 5.3: Mean number of seeds per capitulum of G. ciliata and G. parviflora grown from different sowing densities at two soil moisture regimes and textures.

Species	Mois- ture regime	Clay loam soil					Sandy loam soil				
		Sowing densities per pot				Mean ±S.E.	Sowing densities per pot				Mean ±S.E.
		10	30	90	270		10	30	90	270	
<u>G. ciliata</u>	High	17.6	17.0	16.8	17.5	17.2±0.2	18.8	17.2	16.5	15.3	16.9±0.7
	Low	15.7	17.2	16.5	15.8	16.3±0.3	18.6	18.8	16.2	16.1	17.4±0.7
<u>G. parviflora</u>	High	29.0	26.8	27.0	24.0	27.2±1.0	28.5	26.6	26.2	24.0	26.3±0.3
	Low	26.5	25.0	24.6	24.0	25.0±0.5	26.3	26.3	26.0	25.0	25.9±0.3
	Mean ±S.E.	22.2 ±3.2	21.5 ±2.6	21.2 ±2.7	20.3 ±2.2		23.0 ±2.6	22.2 ±2.5	21.2 ±2.8	20.1 ±2.5	

Source of variation	Probability	Source of variation	Probability
Species	< 0.01	Soil texture	Not significant
Moisture regime	Not significant	Density	Not significant
Soil texture	Not significant	Soil texture x density	Not significant
Species x moisture regime	Not significant	Error	Not significant
Moisture regime x soil texture	Not significant		
Species x soil texture	Not significant		
Species x moisture regime x soil texture	Not significant		

both the species) (Table 5.4). The ratio was greater in sandy loam soil than that in clay loam soil for both the weeds. However, the effect of interaction of any two factors was insignificant with the exception of moisture regime x soil texture.

Reproductive effort

Reproductive effort expressed as the mean number of seeds/g biomass (Bazzaz & Carlson, 1979) showed a negative correlation with increasing population density in both species (Fig. 5.7). However, the value of G. ciliata was relatively higher than that for G. parviflora, the difference being significant ($p < 0.05$) at all densities in clay loam soil and at low densities in sandy loam soil at high moisture level. (The moisture stress caused a significant reduction ($p < 0.01$) in reproductive effort of both species irrespective of soil texture. G. parviflora showed greater reproductive effort in sandy loam soil as compared to clay loam in the high moisture regime (Fig. 5.7).

Total biomass:

(Total biomass/pot of both species increased with population density (Fig. 5.8) but this was not proportional with increase in density. Any increase in density beyond 16 plants/pot resulted in either constant or reduced biomass per pot of G. parviflora (Fig. 5.8). Populations of both weeds grown in sandy loam soil gave significantly ($p < 0.05$) better yield than

Table 5.4: Seed output/input ratio of G. ciliata and G. parviflora in relation to sowing density at two soil moisture regimes and textures.

Species	Moisture regime	Clay loam soil					Sandy loam soil				
		Sowing densities per pot				Mean \pm S.E.	Sowing densities per pot				Mean \pm S.E.
		10	30	90	270		10	30	90	270	
<u>G. ciliata</u>	High	54.8	21.2	9.6	2.9	21.1 \pm 11.5	71.7	23.6	9.6	2.6	26.8 \pm 15.5
	Low	6.6	2.5	1.0	0.3	2.6 \pm 1.4	9.9	4.1	1.4	0.4	3.9 \pm 2.1
<u>G. parviflora</u>	High	35.4	13.5	4.2	1.0	13.5 \pm 7.7	68.9	27.6	6.5	1.7	26.2 \pm 15.3
	Low	4.4	1.8	0.6	0.2	1.8 \pm 0.9	5.7	3.2	1.2	0.3	2.6 \pm 1.2
	Mean \pm S.E.	25.3 \pm 12.1	9.8 \pm 4.6	3.9 \pm 2.1	1.1 \pm 0.6		39.0 \pm 18.1	14.6 \pm 6.4	4.7 \pm 2.0	1.3 \pm 0.6	

Source of variation	Probability	Source of variation	Probability
Species	Not significant	Soil texture	< 0.05
Moisture regime	< 0.01	Density	< 0.01
Soil texture	< 0.05	Soil texture x density	Not significant
Species x moisture regime	Not significant	Error	Not significant
Moisture regime x soil texture	< 0.05		
Species x soil texture	Not significant		
Species x moisture regime x soil texture	Not significant		

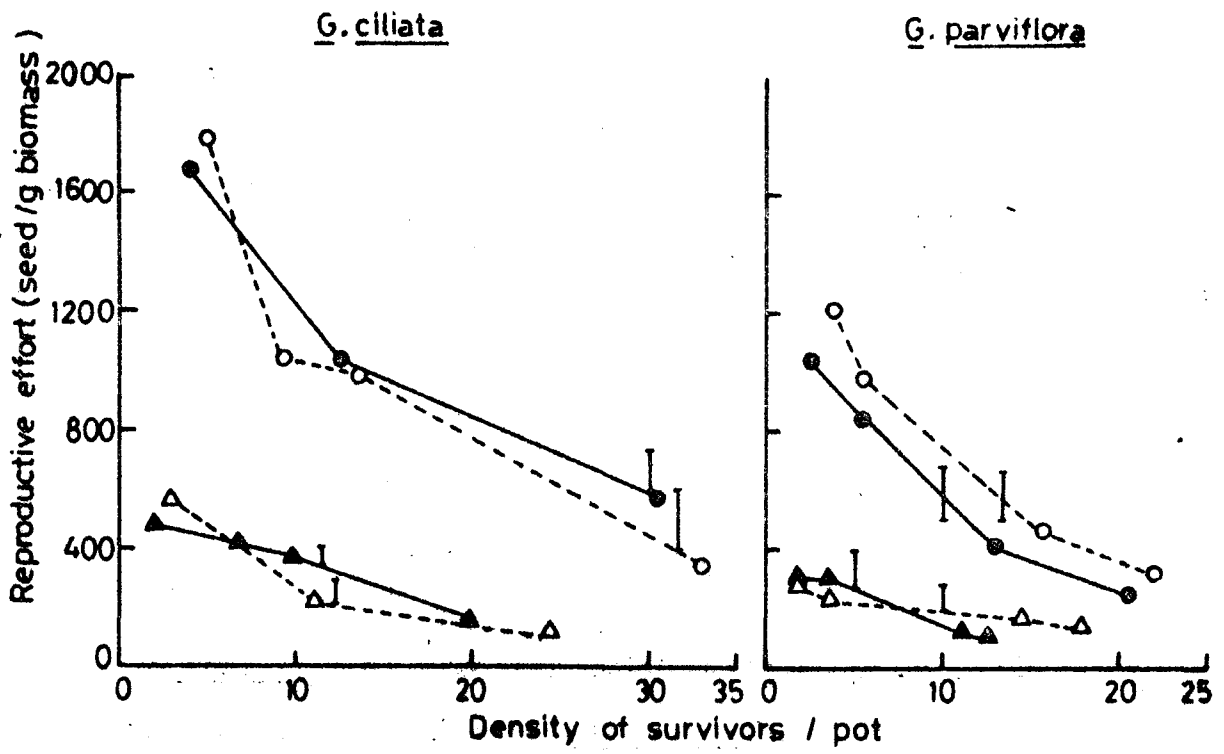


Fig. 5.7

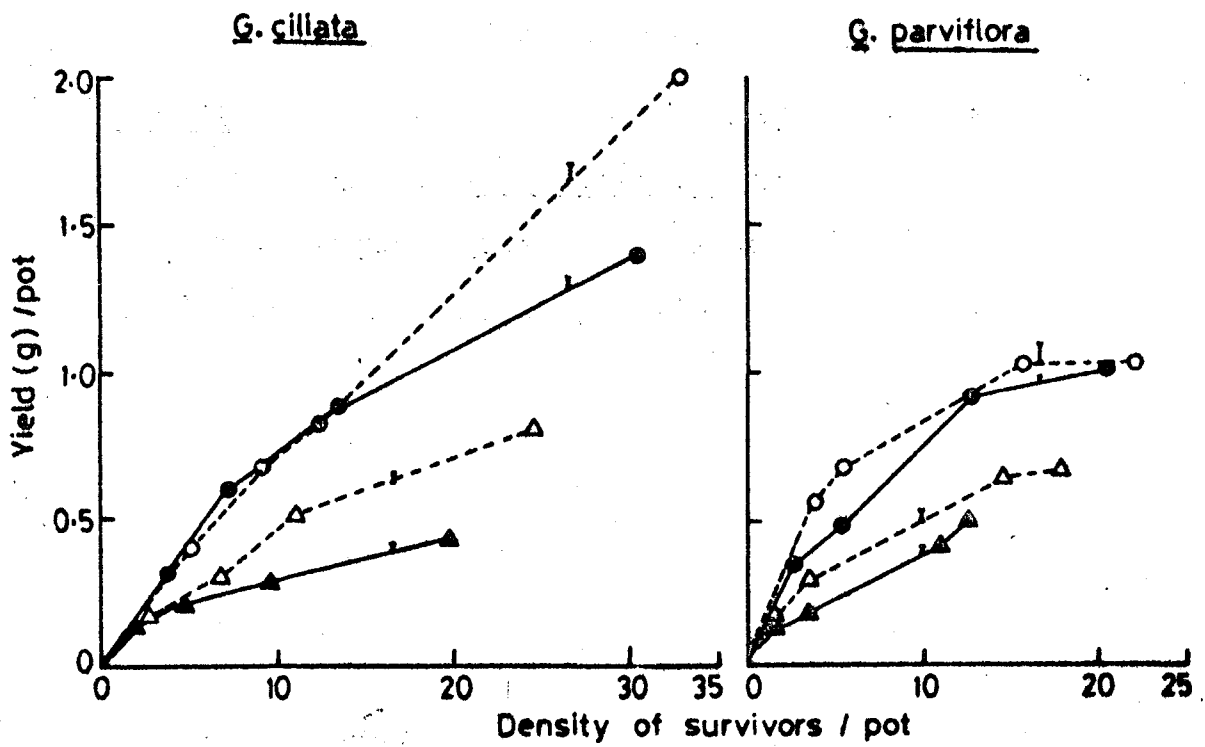


Fig. 5.8

in the clay loam soil. Moisture stress caused a significant reduction in total biomass ($p < 0.05$).

Total biomass/plant successively decreased with increase in population density ($p < 0.01$) (Table 5.5). Biomass/plant of G. parviflora was significantly ($p < 0.05$) higher than that of G. ciliata. The biomass per plant of G. parviflora was greater in sandy loam than in clay loam soil. Moisture stress caused a significant reduction ($p < 0.01$) in plant biomass of both weeds but the decrease was more pronounced in case of G. ciliata at high density (Table 5.5).

DISCUSSION

Results on seed germination in relation to sowing density indicate that increased seed input to the soil does not always ensure the same degree of increase in seedling population. Such reductions in seed germination provide a regulatory mechanism to populations as has been argued by Palmblad (1968a). According to Harper (1961) and Yadav & Tripathi (1981), seed germination and establishment of a plant species is determined by the interaction of soil seed bank and available "safe microsites". Relatively poor germination of both weeds in this study at low moisture level signifies the role of soil moisture in their germination. The increased germination of clumped seeds, as seen in the experiment, has also been observed for several other plant species (Ballard, 1958; Linhart & Pickett, 1973; Linhart, 1976; Waite & Hutchings, 1978). Conversely, in certain species,

Table 5.5: Total biomass (mg) per plant of G. ciliata and G. parviflora grown from different sowing densities at two soil moisture regimes and textures.

Species	Moisture regime	Clay loam soil				Mean \pm S.E.	Sandy loam soil				Mean \pm S.E.
		Sowing densities per pot					Sowing densities per pot				
		10	30	90	270		10	30	90	270	
<u>G. ciliata</u>	High	82.9	80.3	62.1	38.9	66.0 \pm 10.2	85.1	72.3	64.5	58.2	70.3 \pm 5.8
	Low	59.2	41.5	31.2	22.9	38.7 \pm 7.8	60.5	45.3	41.6	25.6	43.2 \pm 7.1
<u>G. parviflora</u>	High	132.2	90.4	72.5	52.4	86.8 \pm 17.0	153.4	124.4	78.5	57.9	103.5 \pm 21.6
	Low	81.2	49.6	39.2	38.4	52.1 \pm 10.0	102.3	81.7	44.9	37.2	66.5 \pm 15.3
	Mean \pm S.E.	88.8 \pm 15.4	65.4 \pm 11.8	51.2 \pm 9.6	38.1 \pm 6.0		100.3 \pm 19.6	81.1 \pm 16.3	57.4 \pm 8.6	34.7 \pm 8.0	
Source of variation		Probability				Source of variation		Probability			
Species		< 0.05				Soil texture		Not significant			
Moisture regime		< 0.01				Density		< 0.01			
Soil texture		Not significant				Soil texture x density		Not significant			
Species x moisture regime		< 0.05				Error		Not significant			
Moisture regime x soil texture		Not significant									
Species x soil texture		Not significant									
Species x moisture regime x soil texture		Not significant									

seed clumping results in decreased germination (Palmlblad, 1968a; Linhart, 1976). The positive germination response to clumping of seeds has been attributed by Linhart (1976) to physiological factors (possibly through production of certain chemicals) and/or to the combined force of several simultaneously growing radicles that may help them emerge. Relatively better germination of the two weeds in sandy loam soil as observed in the present study conforms with the findings of Waite & Hutchings (1978) and the probable cause may be the better aeration due to preponderance of larger pores which facilitate seedling emergence.

Seed output from the population does not only depend on seed input but also on the events that control different physiological processes starting with the germination of the buried seeds to seed setting by the plants grown from these. At each stage of life cycle there may be successive elimination of individuals from the population either through mortality or through poor growth. The plants showing plasticity may **not** all reproduce successfully as observed in the present study (Fig. 5.3). Wastage of resources by non-reproducing individuals may be critical particularly in situations where the production of seeds is lesser than the number of seeds sown. If non-reproducing individuals persist for a long time as observed in the present study the maintenance of populations may be rendered rather more difficult. Very low production of seeds by both weeds at high sowing densities under low moisture level

resulting in low seed output/input ratio (<1) demonstrates that the population regulation may depend on sowing density and soil moisture. In such cases the population size will keep on shrinking under environmental constraints. Mortality in the dense population grown at high moisture level occurred relatively earlier as compared to the low density populations, which may be attributed to the shade cast due to better growth of early emerging individuals. This illustrates the significance of emergence time in seedling fitness as suggested by Ross & Harper (1972), Ford (1975), Harper (1977) and Howell (1981). Seedling mortality in both weeds was observed to be density-dependent (Fig. 5.2) indicating that the fate of an individual is determined by the space available to it, to feed upon the resources present there (Ross & Harper, 1972; Inouye, 1980), as is also reflected by the better seedling survival under the scattered pattern of sowing. Self-thinning in response to increasing density as reported by earlier workers (Yoda et al., 1963; Palmblad, 1968a; White & Harper, 1970; Tripathi & Gupta, 1980) was observed in the two weeds.

Plastic reduction in reproductive growth of the two weeds caused by an increase in population density and moisture stress (Fig. 5.3) also imposes restrictions on further growth of their populations. Decrease in fertility with increasing population density has been reported in many species e.g. Agrostemma githago (Harper & Gajic, 1961), Avena fatua and A. barbata (Marshall & Jain, 1969), Arabidopsis thaliana (Myerscough & Marshall, 1973) and Bothriochloa pertusa and

Dichanthium annulatum (Tripathi & Gupta, 1980). The reproductive effort of both weeds also declined at high sowing densities which conforms with earlier results pertaining to decrease in production of seeds and propagules due to increase in population density observed in Tussilago farfara (Ogden, 1974), Chamaesyce hirta (Snell & Burch, 1975), Sorghum halepense (Williams & Ingber, 1977) and B. pertusa and D. annulatum (Tripathi & Gupta, 1980). Reproductive output per unit area varied with density at high soil moisture level while at low moisture level it remained almost constant over a range of densities which indicates that both species of Galinsoga growing in dense populations on relatively drier habitats in field conditions may show restricted seed production.

The response of the two weeds to changes in soil moisture and texture and increasing population density reveals that these factors affect seed germination, seedling survival and growth of surviving individuals in varying degrees. The yield per unit area increased with the population density in G. ciliata but in G. parviflora it was almost levelled off at D_{16} (Fig. 5.8) showing that G. ciliata may absorb a greater stress caused by density increase. However, the yield of G. ciliata showed greater reduction due to decrease in soil moisture with increased proportion of sand in soil thus indicating differential response of the two weeds to soil moisture and texture. The population of potential offspring of the two weeds is also regulated due to restriction imposed by these factors on number of reproducing individuals and seed production

as has also been argued by Harper (1977). For example, soil moisture stress caused so much reduction in seed production that the seed output was even less than the number of seeds sown, especially at high densities (Fig. 5.5). The reduced proportion of sand in the soil caused 50% reduction in seed production particularly in G. parviflora thus indicating the significance of soil texture in population regulation. Such a reduction in seed output may be mediated either through low nitrogen content of the clay loam soil (Table 5.1) as has been observed by Tripathi & Yadav (1982) in case of Eupatorium spp., and/or through reduced level of available soil moisture in clay rich soils (Kramer, 1969). The effect of various physical factors was exaggerated at high population densities which shows that the severity of intraspecific competition coupled with the environmental constraints operating at different stages of the life cycle contributes a great deal to the population regulation of these weeds.

CHAPTER VI

Effect of density and soil nitrogen on population regulation
of Galinsoga spp. grown in pure and mixed stands.

INTRODUCTION

Role of density in population regulation of plants has been emphasized by Sukatchev (1928), Tadaki & Shedei (1959), Harper & Gajic (1961), Yoda et al. (1963), Myerscough & Marshall (1973), Harper (1977) and Tripathi & Yadav (1982) and its effect on the reproductive capacity has been studied by Tripathi (1968), Palmblad (1968a), Khan & Bradshaw (1976), Williams & Ingber (1977), Watkinson & Harper (1978), Weiss (1978), Barkham (1980), Tripathi & Gupta (1980) and White & Hutchings (1982), but not much attention has been paid to the studies on inter-plant variation in pure and mixed population at varying density levels. Stern (1965) and Obeid et al. (1967) found that populations initially showing a normal distribution of plant weights, later developed a skewed distribution and the skewness was exaggerated at high population density. It has been shown that biomass density relationship in pure populations follows the $-3/2$ power law of Yoda et al. (1963). Later, it was observed that the $-3/2$ power law is also applicable in case of mixed population of morphologically similar species (White & Harper, 1970). Bazzaz & Harper (1976) tested the thinning law using mixed populations of two contrasting species grown at two fertility levels.

It was thought that a study of the response of pure and mixed populations of two cohabiting species to soil nitrogen and population density could be interesting. Thus the present study was made using the two sympatric annual weeds viz., Galinsoga

ciliata and G. parviflora. Besides, their population regulation and co-existence in nature have also been discussed in light of inter-plant variation in weight and capitula production.

MATERIALS AND METHODS

(Mature seeds of G. ciliata and G. parviflora were collected in November 1980 from natural populations growing in Shillong. These seeds were air dried and stored in polythene bags at room temperature (12°C-18°C).

The experiment was designed as a factorial of 4 densities of the two species at two soil nitrogen levels in pure and mixed stands with three replicates. The seeds were sown in plastic pots (internal diam. 21 cm with a basal hole for drainage) on 6 April 1981 to raise the pure and mixed populations. After seedling emergence, thinning was done on 26 April 1981 to get the four densities viz., 4, 12, 36 and 108 plants per pot (equivalent to 120, 360, 1080 and 3240 plants per m²). By this time, seedlings of both the species were clearly distinguishable (by the presence of hairs on body surfaces of G. ciliata and their absence in case of G. parviflora). In mixture, each of the two species contributed half of the total density in the pot and their seedlings were alternately arranged. Each pot was filled with 4 kg of homogeneously mixed air dried sandy soil. The nitrogen content of the pot soil as estimated by Kjeldahl method (Jackson, 1962) was found to be 0.18% which

represented low soil nitrogen level. High nitrogen level was created by mixing 20.62 g ammonium nitrate per pot before sowing, which raised the soil nitrogen content to 0.36%.

The experimental pots were kept in the net house roofed with polythene sheets for protecting against rain. Each pot was supplied 250 ml of tap water on alternate day, throughout the experimental period, which was found appropriate to keep the soil reasonably moist without causing any leaching of nutrients.

At the end of 4 month long experimental period, the observations were made on number of survivors and fertile plants per pot and number of capitula and seeds per reproducing plant and per unit area. (Per plant and per pot biomass was also estimated. For biomass estimation the individual plants were excavated from pots, washed thoroughly with running water and then weighed.

Regression co-efficients were calculated between number of survivors per pot and mean dry weight per plant and between number of survivors and number of capitula per plant of the two weeds in pure and mixed populations at two nitrogen levels. The frequency distribution of weight and capitula classes were plotted at density 12, 36 and 108. Based on the range of variation, ten weight classes and eight capitula classes were recognised in both weeds at a given density.

RESULTS

Plant mortality:

There was no mortality at density 4 and 12, but at higher densities both weeds showed mortality which tended to increase at high nitrogen level (Fig. 6.1). G. parviflora experienced greater mortality than G. ciliata. The two species generally showed either equal or increased survival in mixture as compared to the corresponding pure population. However, G. parviflora grown at highest density showed slightly lower survival in mixture than in monoculture (Table 6.1).

Biomass accumulation:

Biomass per plant of both weeds decreased with increase in population density but the regression co-efficients were considerably lower than the theoretical value of -1.5 as predicted by the thinning law (Fig. 6.2). Irrespective of soil nitrogen, the two weeds showed relatively greater value of 'r' in mixture than in pure. Frequency, distribution curves for biomass were close to the expected normal distribution at density 12, but further increase in density resulted in skewed distribution (Fig. 6.3). The skewness of biomass distribution was more marked in G. parviflora than in G. ciliata. However, increased soil nitrogen reduced the degree of plant biomass skewness in both weeds

Fig. 6.1: Plant mortality of G. ciliata (C) and G. parviflora (P) in relation to soil nitrogen and population density in pure and mixed stands. The filled columns represent pure stand and open columns mixed stands.

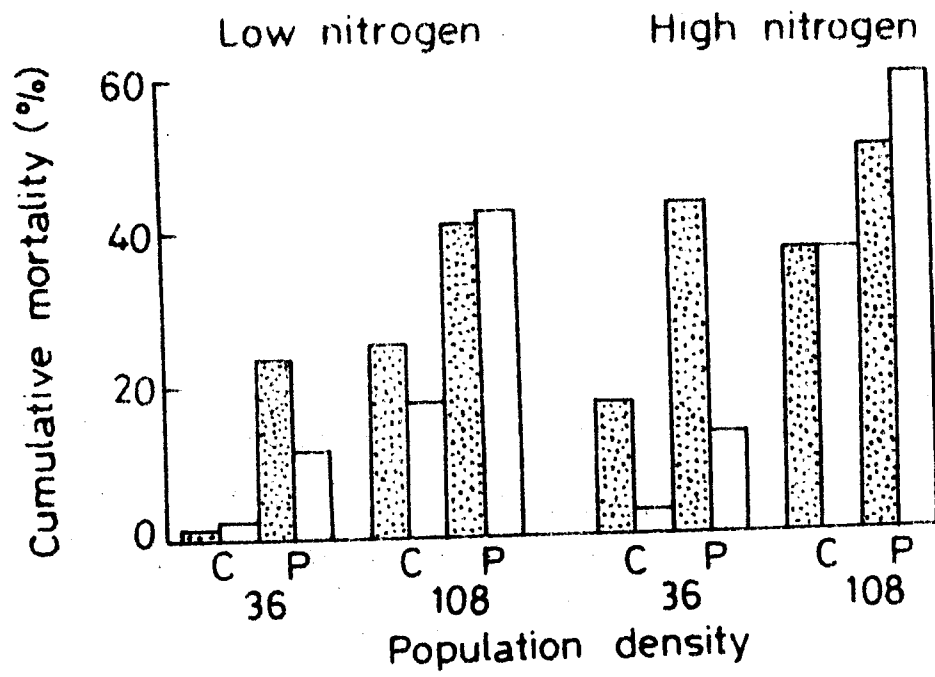


Fig. 6.1

Table 6.1: Percentage increase (+) or decrease (-) in survival, yield and seed output of G. ciliata and G. parviflora in mixed populations as affected by population density and soil nitrogen levels.

Soil Nitrogen levels	Density per pot	<u>G. ciliata</u>			<u>G. parviflora</u>		
		Survival	Yield	Seed output	Survival	Yield	Seed output
Low	4	0	-7.96	-20.43	0	+10.74	-39.90
	12	0	+6.02	+43.10	0	+13.28	-26.78
	36	+0.06	+28.23	+77.05	+11.11	+42.23	-4.01
	108	+8.04	+13.20	+92.23	-2.15	-12.96	-11.55
High	4	0	+2.39	0	0	+0.36	-39.38
	12	0	+25.77	+59.24	0	+0.49	-8.57
	36	+14.73	+46.19	+69.59	+29.44	+0.85	-47.74
	108	0	+36.84	+61.58	-9.07	-28.46	-17.64

Fig. 6.2: Relationship between per plant biomass and number of survivors of G. ciliata and G. parviflora as affected by soil nitrogen level and stand nature. Continuous lines represent the value in pure stands and broken lines in mixed stands.

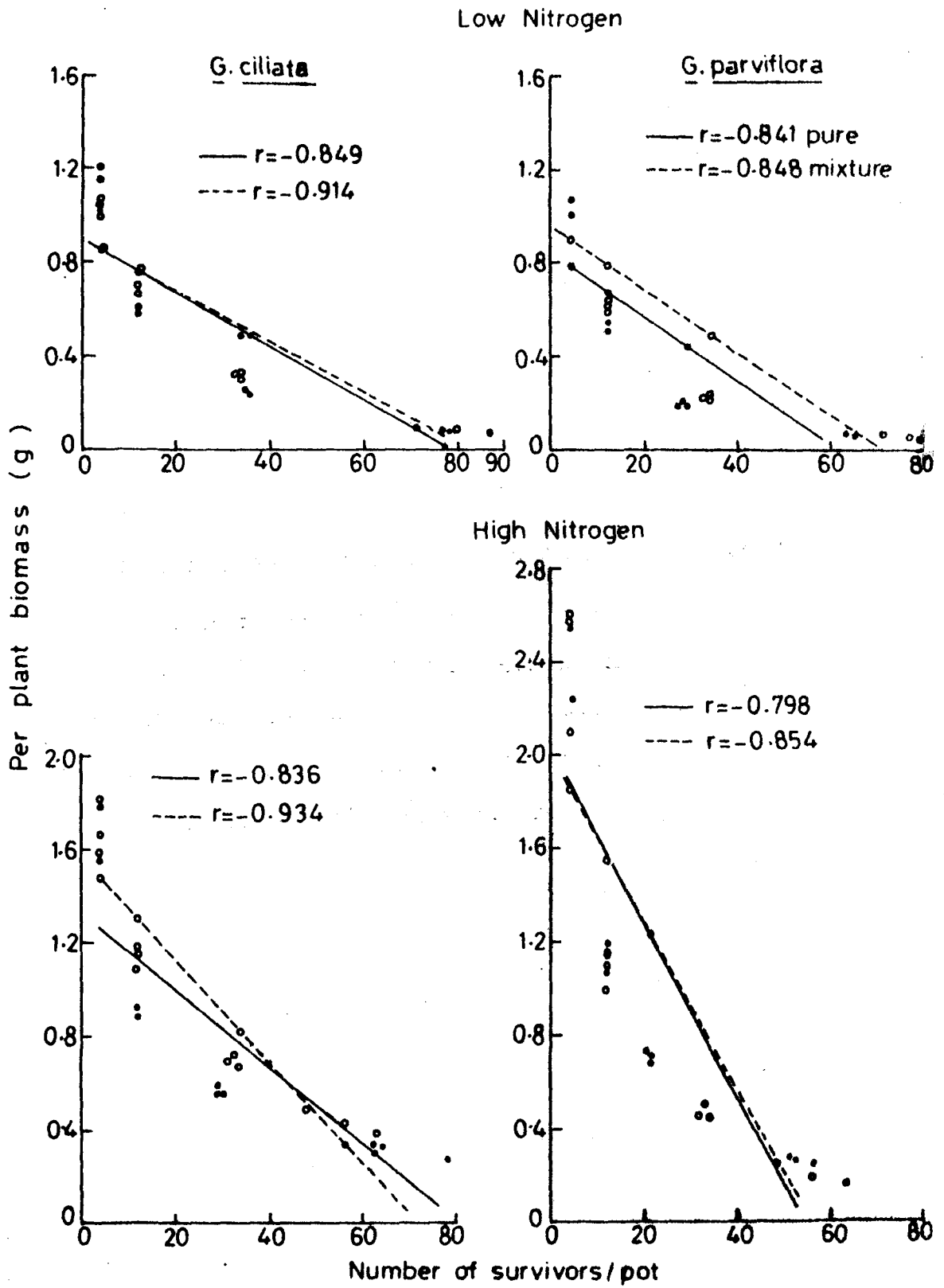


Fig. 6.2

Fig. 6.3: Frequency distribution of plant biomass of G. ciliata and G. parviflora in relation to soil nitrogen and population density in pure and mixed stands. C and P represent the pure populations of G. ciliata and G. parviflora and M represents the mixed stand.

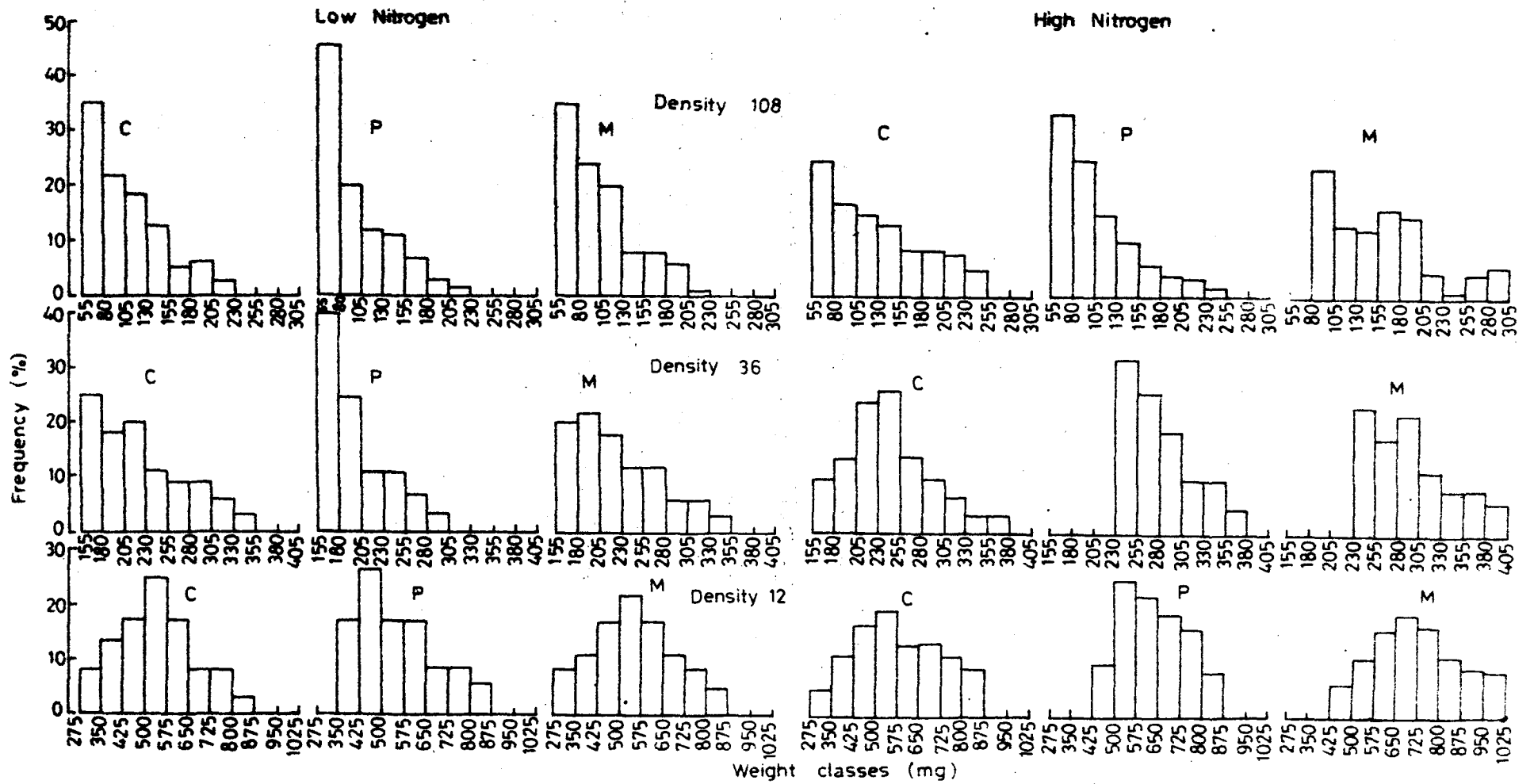


Fig. 6.3

Per pot yield in pure population of G. ciliata was maximum at density 36 and 108 at low and high nitrogen levels respectively while in G. parviflora the corresponding maxima were recorded at density 12 and 36 (Fig. 6.4). The combined yield of the two weeds in mixture was maximum at density 36 irrespective of soil nitrogen.) In general, both species exhibited better yield when grown either at high nitrogen level or in mixture with the exception of G. parviflora grown at highest density, where it showed c.13% and 29% reduction in yield in mixture vis-a-vis its yield in pure at low and high nitrogen levels respectively (Table 6.1). Percentage contribution of the two weeds to the mixture yield was also modified by density; at low density (D_4) G. parviflora contributed more than 50% of total yield, but with increase in density the percentage contribution of G. ciliata increased so much so, that at highest density (D_{108}) it contributed 2/3rd and 3/4th of the total yield in mixture under low and high nitrogen regimes respectively (Table 6.2).

Percentage fertile plants:

Percentage fertile plants in both weeds decreased with increasing density (Fig. 6.5), but the decrease was much more pronounced in G. parviflora. In contrast to G. parviflora, G. ciliata population showed greater fertility percentage when grown either at high nitrogen level or in mixture.

Fig. 6.4: Total yield per pot of G. ciliata and G. parviflora in relation to population density and soil nitrogen level in pure and mixed stands. Triangles and circles respectively represent the value of G. ciliata and G. parviflora; rectangles represent the value in mixed stands.

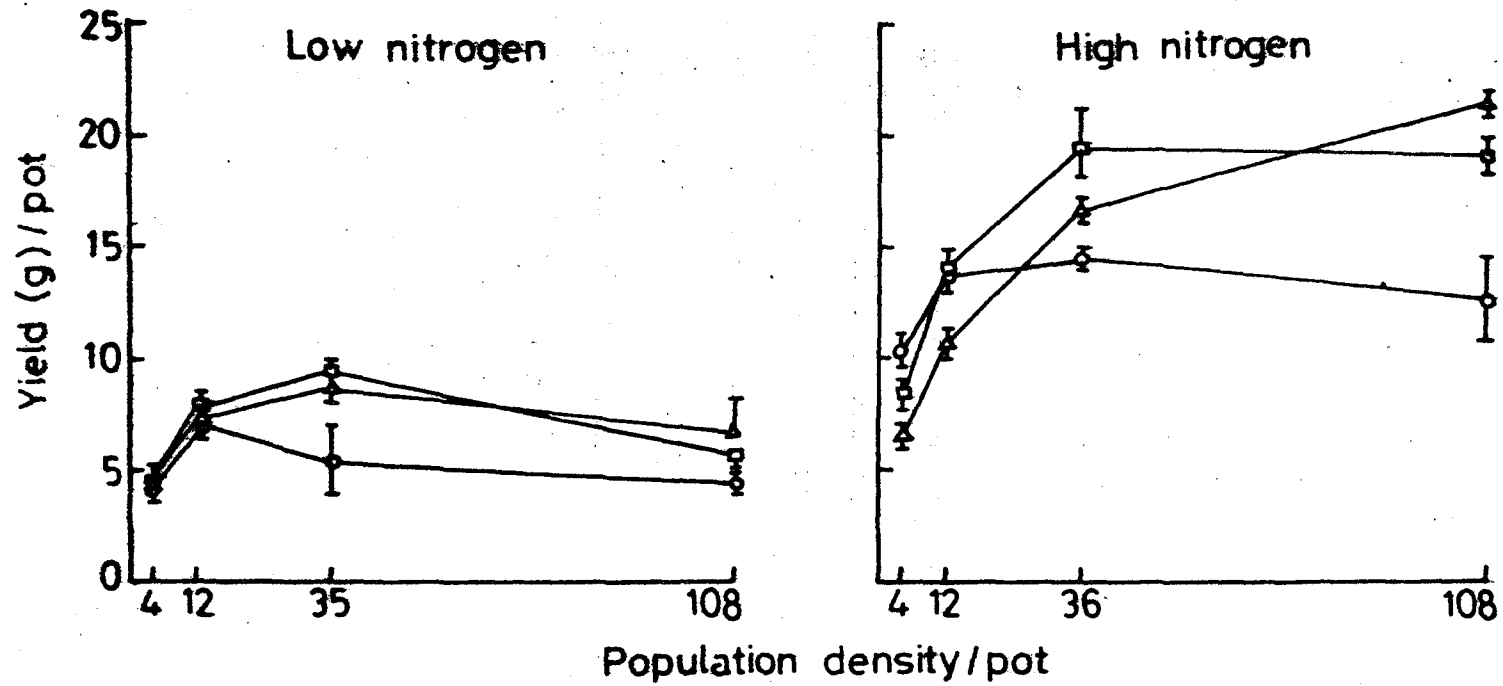


Fig. 6.4

Table 6.2: Percentage contribution of G. ciliata and G. parviflora in mixed population yield and seed output as affected by density and soil nitrogen level.

Soil Nitrogen level	Density per pot	<u>G. ciliata</u>		<u>G. parviflora</u>	
		Yield	Seed output	Yield	Seed output
Low	4	46.33	54.54	53.67	45.46
	12	52.00	78.45	48.00	21.55
	36	59.41	77.43	40.59	22.57
	108	66.22	82.32	33.78	17.68
High	4	39.39	44.26	60.61	55.74
	12	50.00	61.00	50.00	39.00
	36	62.31	76.52	37.69	23.48
	108	77.09	84.25	22.91	15.75

Fig. 6.5: Percentage fertile plants of G. ciliata and G. parviflora in relation to population density. Triangles represent G. ciliata and circles G. parviflora; continuous lines for pure stands and broken lines for mixed stands.

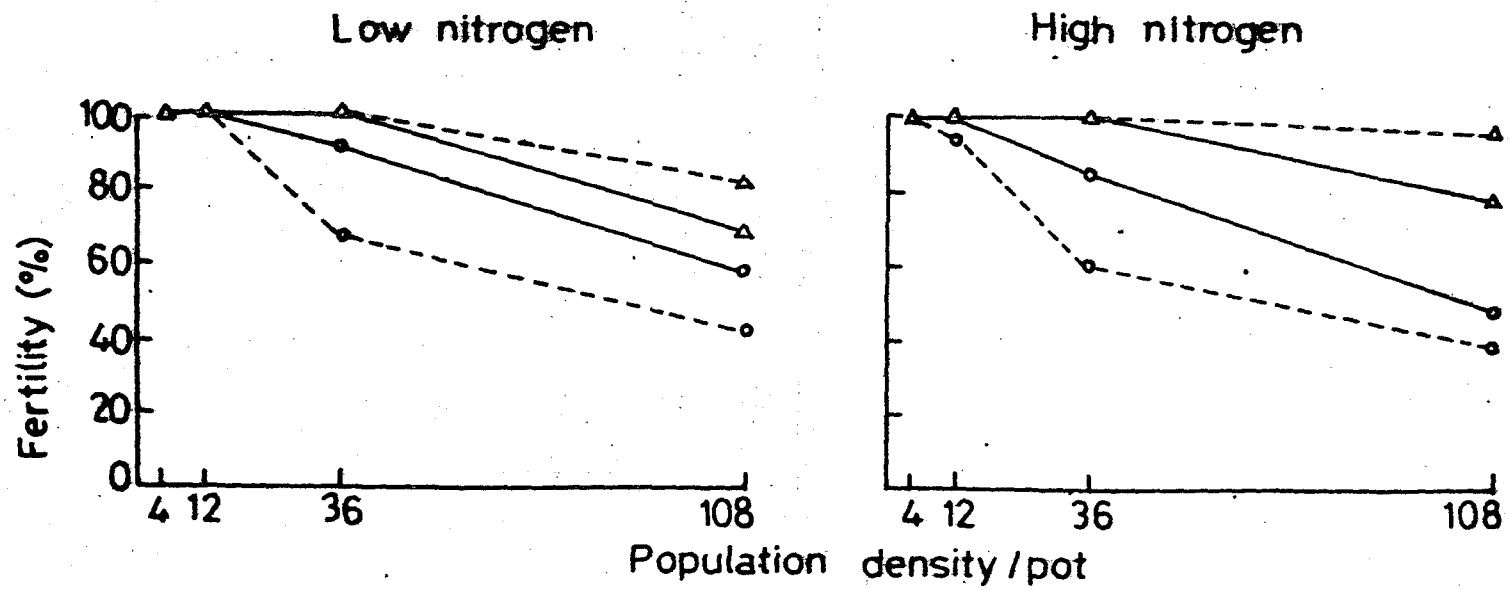


Fig. 6.5

Capitula production:

Number of capitula per plant declined with increasing density but the regression co-efficient was far lesser than the theoretical value (Fig. 6.6). Both species observed higher 'r' value in mixture than in pure except in the case of G. parviflora grown at low nitrogen level. Frequency distribution of capitula of the two weeds showed increased skewness with increase in density (Fig. 6.7). Pure population of G. parviflora exhibited greater skewness than G. ciliata but the skewness was less apparent when the two weeds were grown either together or at high nitrogen level.

Seed production:

The effect of various treatments on number of seeds per capitulum of the two species was insignificant. In both weeds, per plant seed output decreased with increase in population density and decrease in soil nitrogen (Table 6.3), the decrease being more conspicuous in G. parviflora. G. ciliata produced greater number of seeds in mixture than in pure while G. parviflora showed the reverse trend.

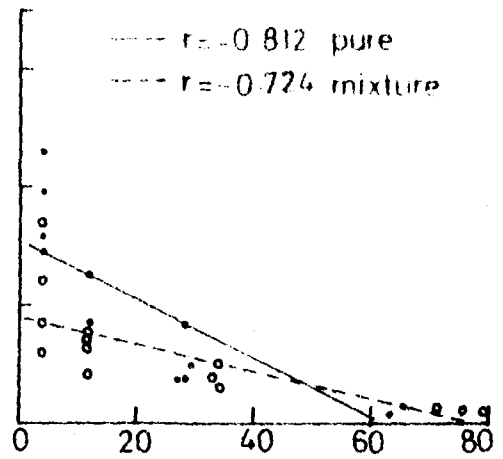
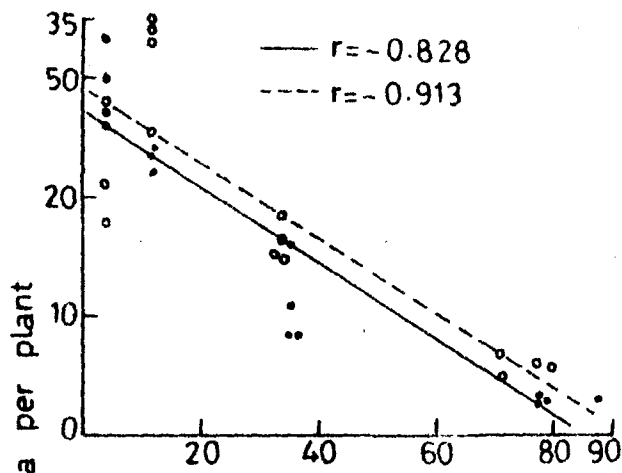
Seed production per pot increased in pure population of G. ciliata with increasing density particularly at high nitrogen level while in G. parviflora the value declined with any increase in density beyond 12 plants per pot (Fig. 6.8). Both species produced much greater number of seeds at high nitrogen

Fig. 6.6: Relationship between number of capitula per plant and density of survivors of G. ciliata and G. parviflora as affected by soil nitrogen in pure and mixed stands. Explanation of the symbols is same as in Fig. 6.2.

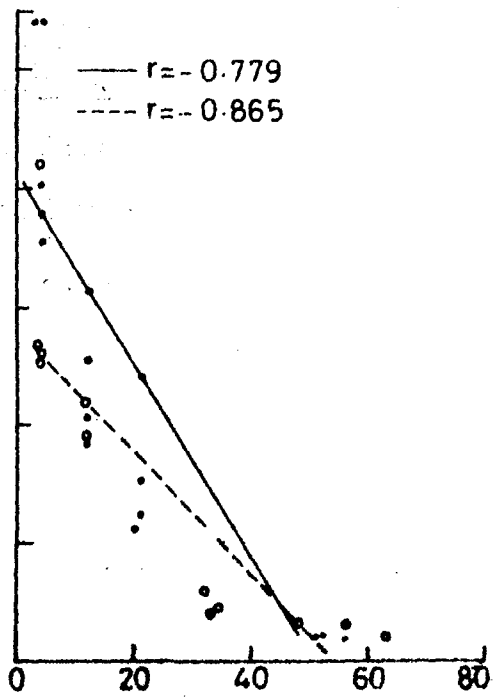
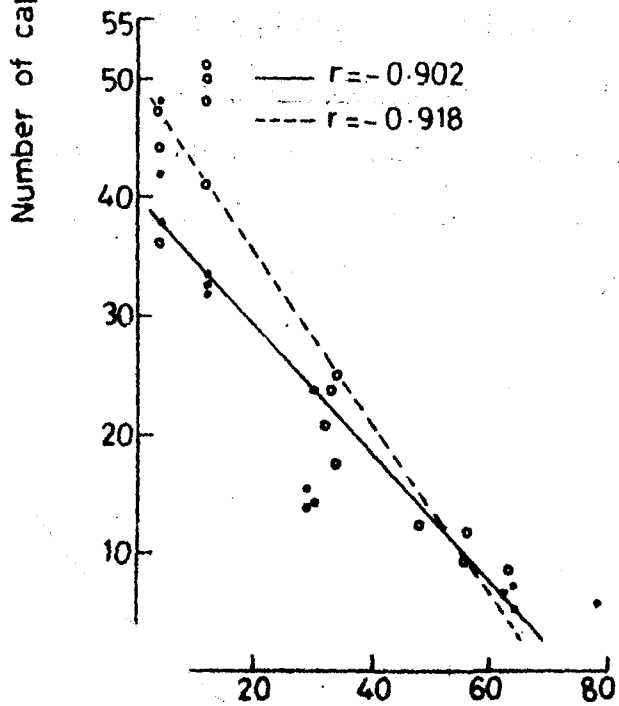
G. ciliata

G. parviflora

Low Nitrogen



High Nitrogen



Number of survivors/pot



PLATE 4.1A

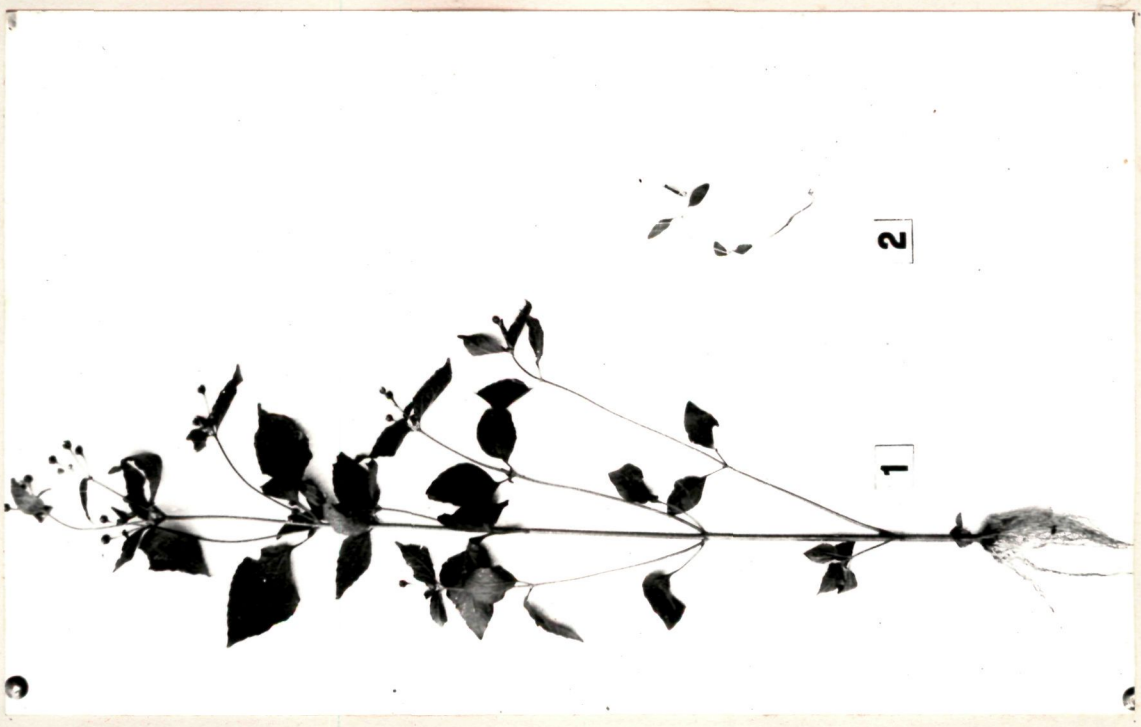


PLATE 4.1B

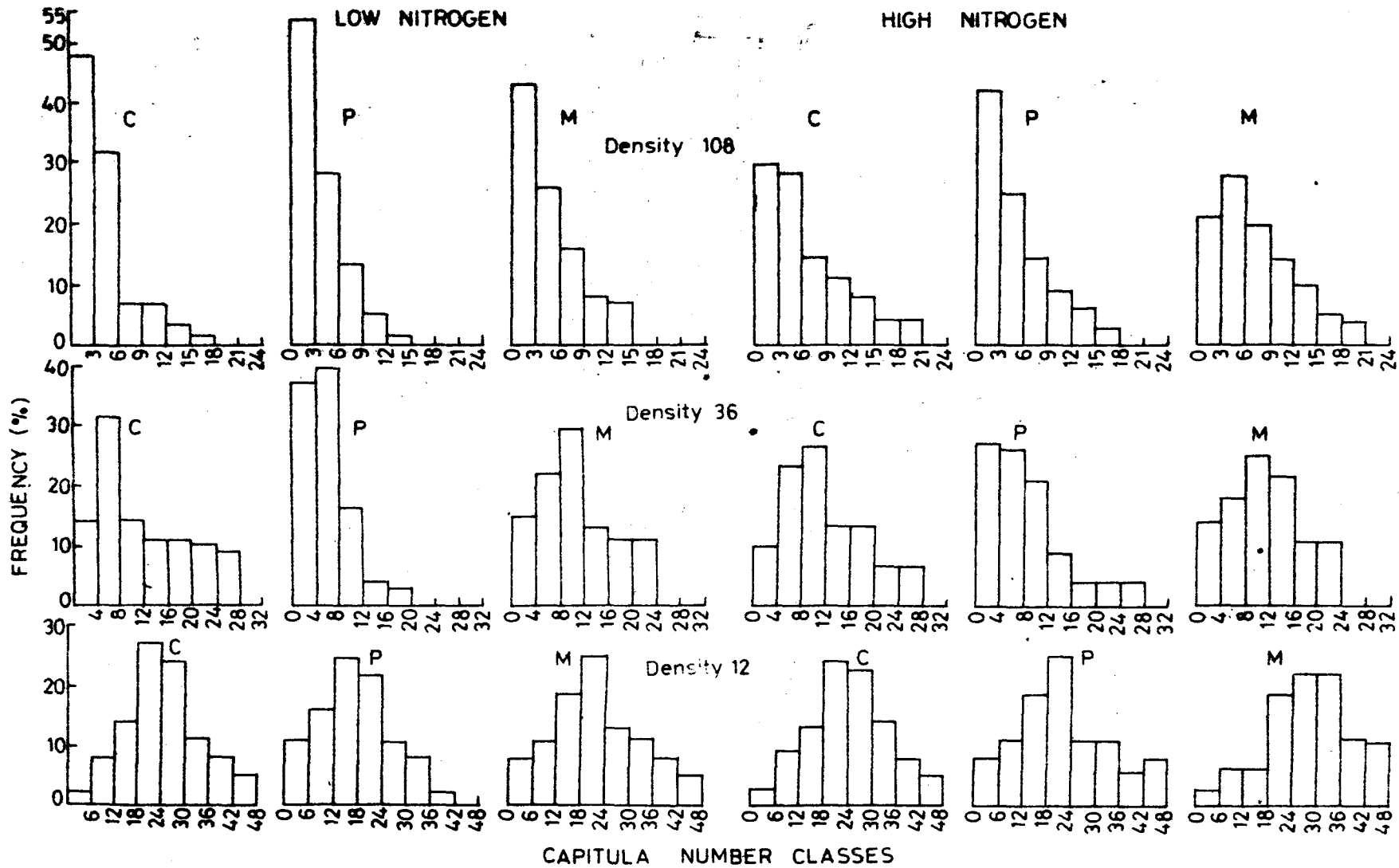


Fig. 6:7

Table 6.3: Number of seeds per plant (\pm S.E.) of G. ciliata and G. parviflora in pure and mixed stands as affected by population density and soil nitrogen levels. (Figures in bracket represent L.S.D. values at $P=0.05$).

Soil Nitro- gen level	Density per pot	<u>G. ciliata</u>		<u>G. parviflora</u>	
		Pure	Mixture	Pure	Mixture
Low	4	422 \pm 38.2	357 \pm 47.5	495 \pm 53.2	297 \pm 81.0
	12	405 \pm 11.9	580 \pm 9.8	272 \pm 28.1	174 \pm 26.5
	36	158 \pm 12.7	262 \pm 10.1	128 \pm 8.9	126 \pm 10.1
	108	81 \pm 3.4	115 \pm 4.7	54 \pm 10.0	68 \pm 5.1
	L.S.D.	(103)	(64)	(97)	(38)
High	4	774 \pm 31.1	753 \pm 57.6	1566 \pm 243.0	949 \pm 161.8
	12	572 \pm 6.8	896 \pm 15.7	631 \pm 55.8	578 \pm 101.2
	36	254 \pm 8.7	353 \pm 32.1	410 \pm 44.1	200 \pm 29.6
	108	133 \pm 3.1	180 \pm 12.2	104 \pm 3.1	130 \pm 14.2
	L.S.D.	(124)	(208)	(316)	(205)

Fig. 6.8: Total seed output of G. ciliata and G. parviflora as affected by soil nitrogen and population density in pure and mixed stands. Explanation of the symbols is same as in Fig. 6.4.

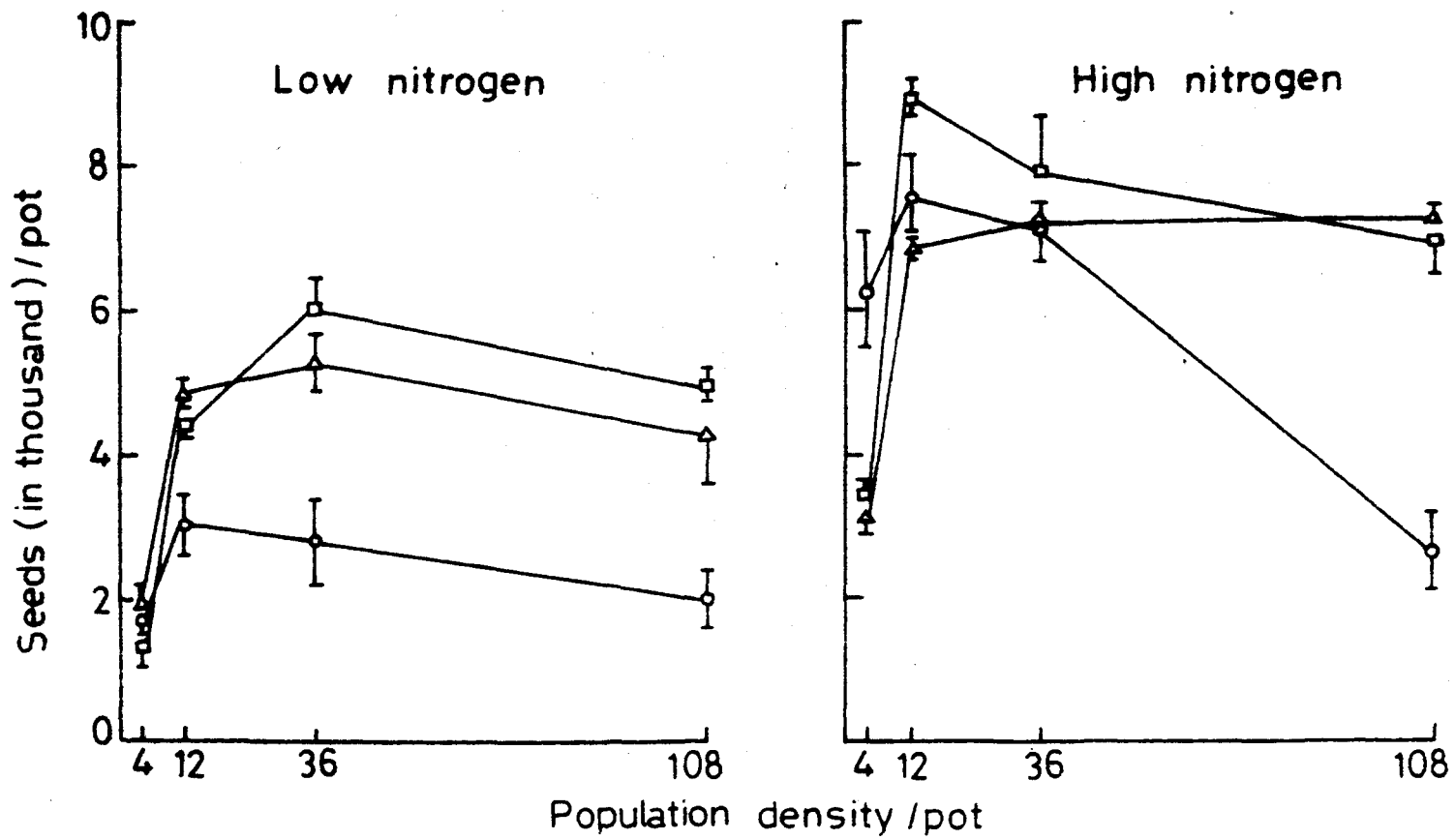


Fig. 6.8

Table 6.4: Percentage abortive capitula per pot of G. ciliata and G. parviflora in pure and mixed stands as affected by population density and soil nitrogen levels.

Soil Nitrogen level	Density per pot	<u>G. ciliata</u>		<u>G. parviflora</u>	
		Pure	Mixture	Pure	Mixture
Low	4	0	0	0	0
	12	0	0	0	0
	36	0	0	7.3	0
	108	0	0	11.9	5.8
High	4	0	0	1.6	0
	12	0	0	3.2	2.2
	36	0.9	0	7.4	17.4
	108	1.8	0.4	20.2	31.6

Table 6.5: Crude reproductive effort of G. ciliata and G. parviflora in pure and mixed stands as affected by population density and soil nitrogen levels.

Soil Nitrogen level	Density per pot	<u>G. ciliata</u>		<u>G. parviflora</u>	
		Pure	Mixture	Pure	Mixture
Low	4	14.3	11.3	10.1	6.4
	12	19.5	26.2	8.1	4.3
	36	13.9	27.5	7.1	6.3
	108	17.9	39.1	7.3	6.4
High	4	14.5	13.9	10.4	6.1
	12	19.1	22.8	9.2	8.7
	36	13.6	15.4	8.9	4.8
	108	10.9	14.4	5.1	4.9

mortality at high fertility level has also been reported by Yoda et al. (1963), White & Harper (1970), Nobel et al. (1979) and Tripathi & Yadav (1982) in other species. At highest density, increased mortality of G. parviflora in mixture over that in monoculture (Fig. 6.1) depicts the importance of G. ciliata in population regulation of the former species in nature where the two weeds often grow together in dense populations.

Although the density increase caused considerable reduction in per plant biomass of the two weeds, the regression co-efficients were far smaller than the expected values showing that the thinning did not occur as a direct result of growth as has been argued by Hutchings & Barkham (1976) and Mohler et al. (1978). Comparatively greater skewness of frequency distribution of biomass in G. parviflora may be linked with the greater competitive suppression in its growth at high density. The reduced skewness of biomass distribution at high nitrogen regime as observed in the present study conforms with the observations of Bazzaz & Harper (1976) for Sinapsis alba and Lepidium sativum. Such a behaviour may be attributed to greater supply of nitrogen which in turn might reduce the intensity of competition. This is also indicated by an increased yield per pot of both species at high nitrogen level.

A comparison of response of the two weeds to increasing density revealed that G. parviflora is more susceptible to density increase. At low density the yield of both species

registered an increase in mixture over their corresponding pure stand yields but at highest density in the mixed populations, G. ciliata became dominant over G. parviflora and reduced the yield of the latter. This might explain as to why the two weeds are seen growing quite well in sparse populations in nature, whereas the dense populations are largely dominated by G. ciliata.

Decreased fertility of the two species in dense populations conforms with the similar response of several other species (Palmlad, 1968a; Williams & Ingber, 1977; Watkinson & Harper, 1978; Weiss, 1978; Tripathi & Gupta, 1980; Tripathi & Yadav, 1982). This may be attributed to intense competition at high density which in turn reduces the number of plants attaining threshold biomass required to start flowering as argued by Thompson & Beattie (1981). In contrast to G. parviflora, a corresponding increase in percentage of fertile plants in the case of G. ciliata grown at high nitrogen level and in mixture reflects better reproductive growth of its population in nitrogen-rich soil and its competitive superiority over the other species.

In both species frequency distribution of capitula was more skewed than that of biomass which may happen because the yield and reproductive growth do not necessarily march hand in hand as argued by Donald (1963) and Clay & Shaw (1981). Like biomass, the frequency distribution for capitula was also relatively more skewed in case of G. parviflora than G. ciliata

showing the greater susceptibility of the former species to density stress. However, the mixture of the two species exhibited lesser skewness which might make their co-existence in nature a little easier.

Although the two weeds produced substantially greater number of seeds at high nitrogen level, they differed in their response to interacting influence of soil nitrogen and crowding. At low nitrogen level seed output of the two weeds tended to decline with any increase in density beyond optimum while at high nitrogen level G. ciliata showed constant increase in seed output with density, indicating that on nitrogen rich habitats increase in density does not restrict the seed production by G. ciliata. The results also suggest that the initiation of capitula development in both species depends upon the factors that favour biomass accumulation while their further growth probably requires different conditions as has also been observed by Tripathi & Yadav (1982) for Eupatorium spp.

One might expect the competitive milieu of an organism to have certain effects on reproductive allocation.

G. parviflora exhibited the inverse relationship between population density and crude reproductive effort as observed by Ogden (1974), Snell & Burch (1975), Abrahamson (1975), Holler & Abrahamson (1977) and Hickman (1977), while the CRE of the other species when grown at low nitrogen regime increased with density, which suggests that with increase in severity of competition the population of G. ciliata devotes

more resources to reproduction, a response exhibited by certain other species under stressed condition (Gadgil & Solbrig, 1972; Hickman, 1975). The CRE of one weed was also influenced by the presence of the other. In contrast to G. ciliata, G. parviflora showed lower CRE value in mixture than in monoculture suggesting that G. ciliata exercises a strong regulatory effect on the population size of the other weed. Such a strategy adopted by G. ciliata coupled with its competitive superiority and better reproductive growth in mixed population enables this weed to dominate over G. parviflora in dense populations in nature. However, the subtle differences in plastic response of the two species to interacting influence of the population density, soil nitrogen and competition between them as observed in this study enables the two weeds to co-exist in nature.

CHAPTER VII

Effect of herbivory on competitive interaction and growth of
G. ciliata and G. parviflora populations

INTRODUCTION

Although herbivory has been reported to play a significant role in the evolution and population dynamics of plants (Gillett, 1962; Ehrlich & Raven, 1964; Fraenkel, 1969; Feeny, 1976; ~~Am~~oades & Cates, 1976), relatively little is known about its specific effects on the growth and reproductive success of plants barring those belonging to the category of crops. Moreover, virtually nothing is known about the effects of interaction between herbivory and congeneric competition (Harper, 1977). It has been shown by several workers (eg. Collins & Aitken, 1970; Maun & Cavers, 1971; Rockwood, 1973; Cates, 1975; Janzen, 1976; Waloff & Richards, 1977; Stephenson, 1978; Lee & Bazzaz, 1980) that manual clipping of foliage causes reduced seed and biomass production. But the response of plants to such simulated defoliations cannot be equated to the effect of herbivory which prevails in natural conditions.

An investigation into herbivory of weedy species may be particularly helpful in evolving an integrated weed control programme by using selected biological control agents. While studying the population dynamics of G. ciliata and G. parviflora it was noticed that in field condition the populations of these weeds were adversely affected due to predation by the foliage-feeding herbivores (slug- Mariaella dussumieri Gray. Pulmonata- Ariophantidae and some Lepidopteron). This prompted to study the relationship between these herbivores and their host,

G. ciliata and G. parviflora, by transplanting the experimental plants into natural environment and by exposing them to natural populations of herbivores. This study was carried out to examine: (i) the effect of the herbivores on the fitness of the two weeds which are predated upon by them; (ii) whether the degree to which the herbivores reduce plant fitness is in any way dependent on the pure and mixed nature of the populations; (iii) the effect of herbivory on the competitive success of the weeds.

MATERIALS AND METHODS

The study was conducted in the experimental field under the thin canopy of the pine stand on the campus of the School of Life Sciences, North-Eastern Hill University, Shillong, between May to September 1981. One half of the experimental field was protected against herbivores by aluminium net (net size = 0.64 m^2) covering, which gave a growth chamber of $2.5 \times 2.0 \times 1.0 \text{ m}$ capacity and the other half was left uncovered, to allow free activity of the herbivores. These two treatments have been henceforth referred as the protected and unprotected plots in the text. In each of the two plots, twelve subplots of size $25 \times 25 \text{ cm}^2$ were delineated in such a way that inter-subplot distance was 30 cm.

Mature seeds of the two weeds, collected from the roadside populations at Shillong in November 1980 were separately kept for germination in shallow trays filled with sandy soil at

25 ± 3°C in BOD incubator. The seedlings were allowed to grow in the trays for 3 days, after which they were transplanted to the experimental plots on 22 May, 1981. The pure and mixed populations of the two weeds were raised to give an overall density of 36 plants per subplot (equivalent to 576 plants/m²), the inter-plant distance being 4 - 5 cm. In mixed population, each of the two species had 18 plants per subplot representing 50% of the total density and the individuals of the two species were planted alternately. The treatments consisted of the pure populations of G. ciliata and G. parviflora and 1:1 mixture of the two weeds in both protected and unprotected conditions. There were 4 replicates for each treatment and the subplots under a given condition were completely randomized. Each subplot was sprayed with equal amount of water on requisite date throughout the study period.

The observations on number of plants damaged by herbivores and finally died in each subplot, were made and compared with the corresponding protected plots. In order to evaluate the effect of feeding damage, a regular and frequent observation on the number of leaves produced by individual plant and leaf area existing at the time of observation was made. For estimation of leaf number and leaf area 8 plants per subplot in pure and 8 plants of each species per subplot in mixture were tagged randomly and their fate was followed. However, the data presented on leaf number and leaf area per plant are means of observations recorded from only 24 plants per treatment as some of the tagged plants also died during experimental period.

Besides, a monthly observation was made at dusk to have an idea about the abundance of herbivores, which is given in Table 7.1.

After 4 months growth when the plants attained maturity, the numbers of capitula and seeds per plant and per unit area were estimated. For dry matter estimation the plants from the plots were excavated whole, the root system was washed thoroughly with a fine jet of running water and the component plant parts were separated, oven dried at 60°C to constant weight and weighed.

RESULTS

Percentage damage and plant mortality:

Although both weeds were considerably damaged by the herbivores and showed an increased mortality in the plot where plants were exposed to predation, G. parviflora suffered more due to herbivory in both pure and mixed stand (Table 7.2).

Vegetative growth:

(a) Leaf production: The plants of G. ciliata subjected to herbivory produced more leaves than those protected from it, while in the case of G. parviflora though in pure stand there was substantial increase in leaf number per plant due to herbivory, in mixture a sharp decrease was observed (Fig. 7.1). However, G. parviflora produced greater number of leaves than G. ciliata.

Table 7.1: Density (per plot) of herbivore of Galinsoga spp. observed in the unprotected plots during study period.

Herbivores	Observation dates; 1981			
	8 Jun.	12 Jul.	12 Aug.	4 Sept.
<u>Mariaella dussumieri</u> Gray	1.75	2.25	1.16	0.84
<u>Pieris napi</u> (Linn.)	0.60	0.66	0.0	0.0
<u>Heliothis armigera</u> Hbn.	0.0	0.84	0.75	0.0
<u>Plutella maculipennis</u> Curt.	0.0	0.0	1.25	1.50
Noctuid larvae	0.0	0.66	1.50	2.17
Unidentified	0.33	0.75	1.08	1.33

Table 7.2: Extent of damage and mortality (\pm S.E.) of Galinsoga as affected by herbivore predation in pure and mixed populations.

Species	Nature of stand	Protected plot		Unprotected plot	
		Damage (%)	Mortality (%)	Damage (%)	Mortality (%)
<u>G. giliata</u>	Pure	0	14.3 \pm 1.4	64.3 \pm 4.2	24.6 \pm 3.4
	Mixture	0	12.7 \pm 4.2	60.3 \pm 3.6	22.2 \pm 3.1
<u>G. parviflora</u>	Pure	0	15.1 \pm 0.8	72.2 \pm 4.6	37.3 \pm 2.9
	Mixture	0	15.9 \pm 1.6	71.3 \pm 5.1	41.2 \pm 1.6

Fig. 7.2: Leaf area per plant of G. ciliata and G. parviflora in pure and mixed stands as affected by the herbivore predation. Explanation of the symbols is the same as in Fig. 7.1.

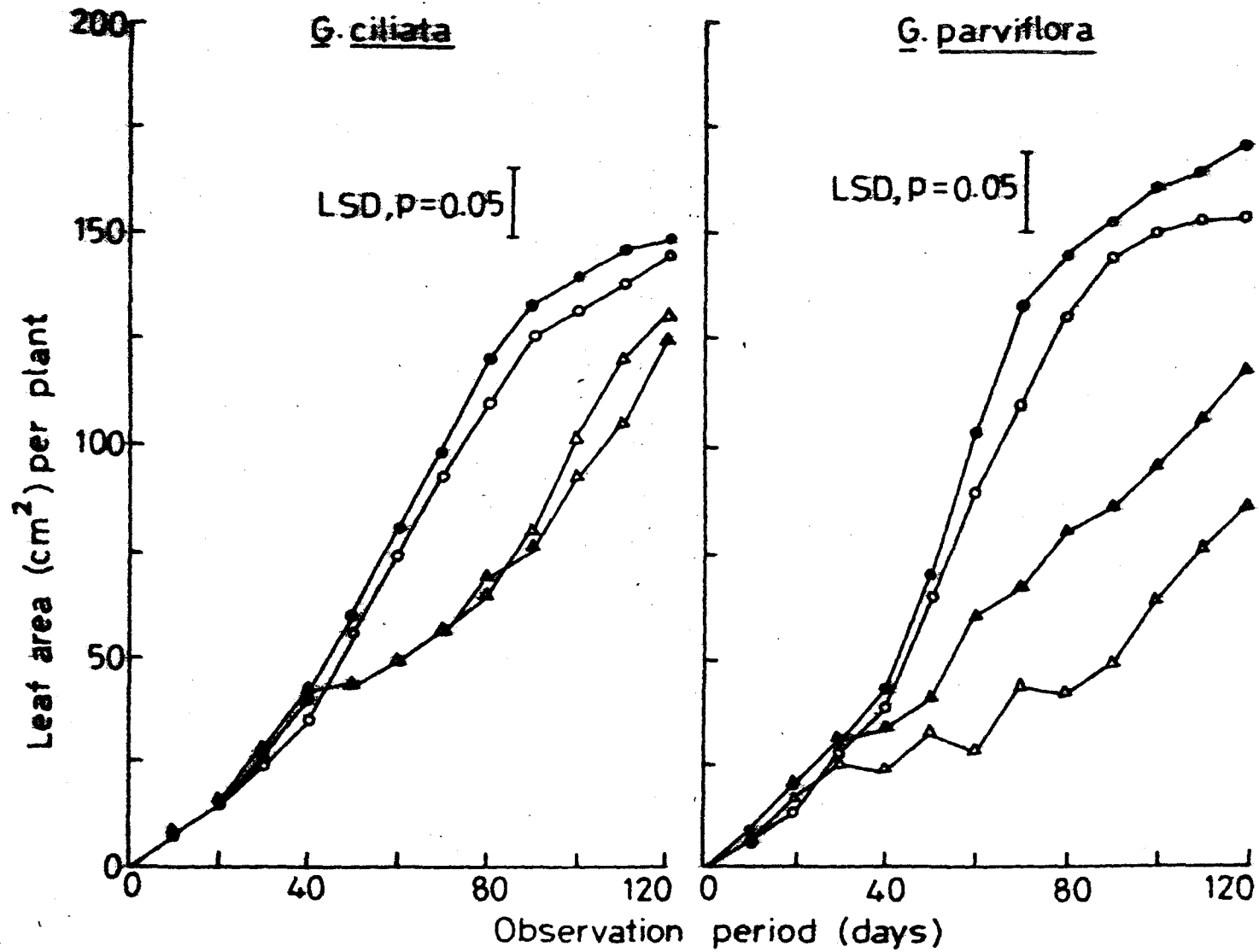


Fig. 7-2

Table 7.3: Percentage reduction in leaf area, seed and dry matter production per plot of G. ciliata and G. parviflora as affected by herbivore predation in pure and mixed populations.

Species	Nature of stand	Leaf area	Seed output	Dry matter yield
<u>G. ciliata</u>	Pure	26.9	30.6	13.6
	Mixture	21.2	24.0	11.8
<u>G. parviflora</u>	Pure	47.8	39.2	31.9
	Mixture	60.9	60.0	53.9

Fig. 7.3: Replacement series diagram based on biomass per pot of G. ciliata and G. parviflora as influenced by the herbivory. Explanation of the symbols: triangles represent yield by G. ciliata and circles by G. parviflora; the filled circles represent combined yield in mixed stand; vertical bars represent S.E. values.

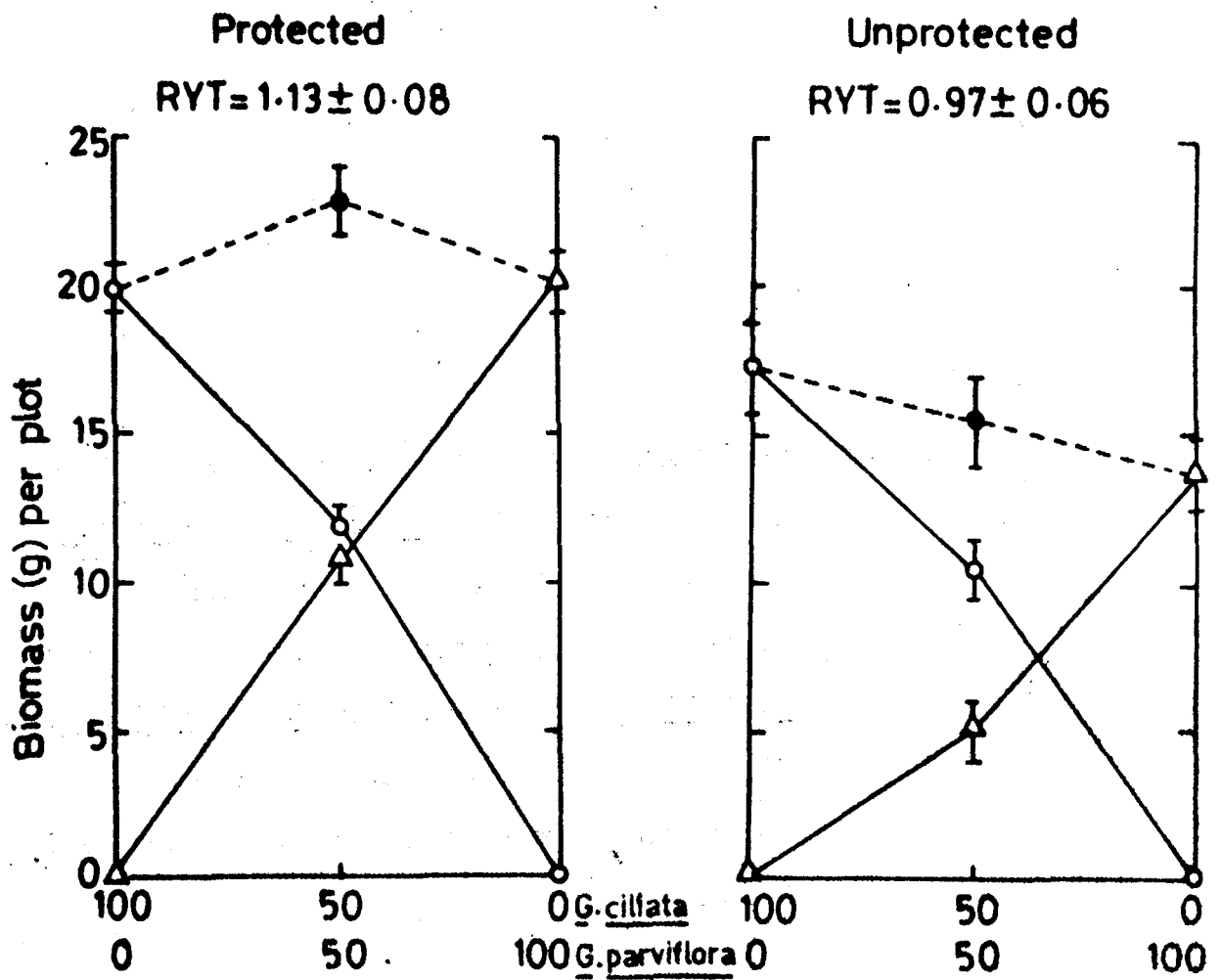


Fig. 7-3

Table 7.4: Reproductive behaviour and biomass (mg) of G. ciliata as affected by herbivore predation in pure and mixed populations.

Character	Protected plot		Unprotected plot	
	Pure	Mixture	Pure	Mixture
No. of capitula/plant	13.5	14.2	11.5	12.4
No. of seeds/plant	247.7	260.1	196.0	220.3
Biomass/plant	648.7	759.2	639.2	751.4
Source of variation	Probability			
	Capitula	Seed	Biomass	
Stand	N.S.	<0.05	<0.05	
Predation	<0.05	<0.05	N.S.	
Stand x predation	N.S.	N.S.	N.S.	
Error	N.S.	N.S.	N.S.	

N.S. = Not significant.

Table 7.5: Reproductive behaviour and biomass (mg) of G. parviflora as affected by herbivore predation in pure and mixed populations.

Character	Protected plot		Unprotected plot	
	Pure	Mixture	Pure	Mixture
No. of capitula/plant	9.7	10.7	8.0	5.8
No. of seeds/plant	242.7	251.2	187.5	140.3
Biomass/plant	659.6	728.0	600.0	489.3
Source of variation	Probability			
	Capitula	Seed	Biomass	
Stand	N.S.	N.S.	N.S.	
Predation	<0.05	<0.05	<0.05	
Stand x predation	<0.05	<0.05	<0.05	
Error	N.S.	N.S.	N.S.	

N.S. = Not significant.

Reproductive growth:

(a) Phenology: Flowering and fruiting in G. ciliata was not influenced either by stand nature or by herbivore predation, while in case of G. parviflora the plants grown in mixture and subjected to predation flowered 20 days later than the protected plants. However, all the plants surviving in the plots flowered during the study period irrespective of herbivory.

(b) Seed production: Per plant capitula and seed production of the two species was considerably reduced due to herbivore predation (Table 7.4 & 7.5). The capitula mortality was, however, nil. Both weeds produced more capitula and seeds in mixture than in pure except in G. parviflora in the mixed population subjected to predation (Table 7.5).

Seed production per plot also exhibited similar trend (Fig. 7.4), but the reduction due to herbivory was more marked in G. parviflora especially in mixed population (Table 7.3).

Resource allocation:

G. parviflora allocated relatively greater biomass to roots as compared to G. ciliata, while the latter allocated more resources towards reproduction (Fig. 7.5). Herbivory caused reduction in resource allocation to leaves in both weeds while the root allocation was reduced only in G. parviflora. However, the resource allocation of the two weeds was independent of stand composition.

Fig. 7.4: Replacement series diagram (based on seed output per pot) of G. ciliata and G. parviflora as influenced by the herbivory. Explanation of the symbols is the same as in Fig. 7.3.

Fig. 7.5: Dry matter allocation of G. ciliata and G. parviflora to different plant parts as affected by herbivory and nature of the stand.

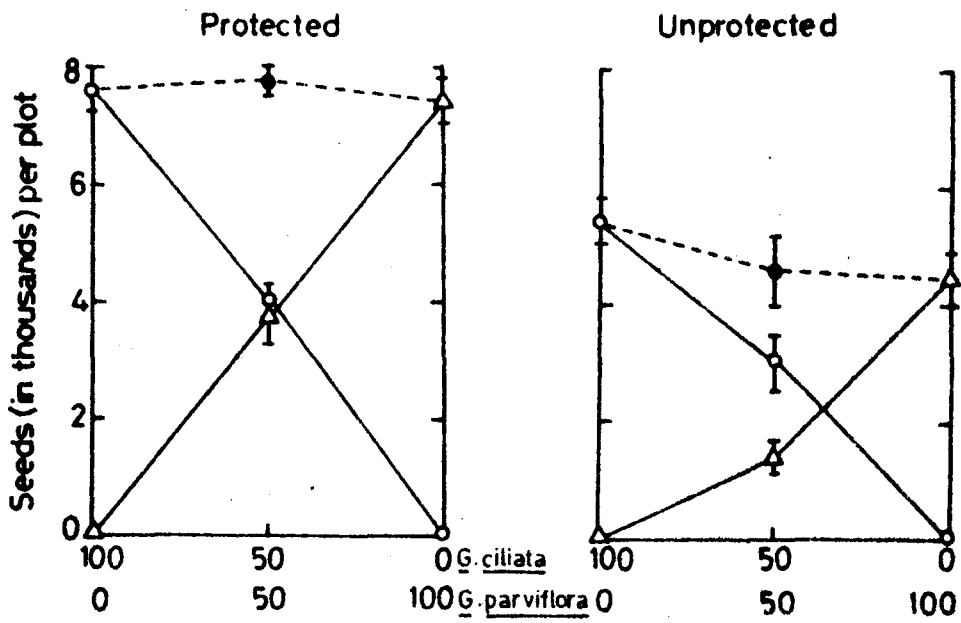


Fig. 7-4

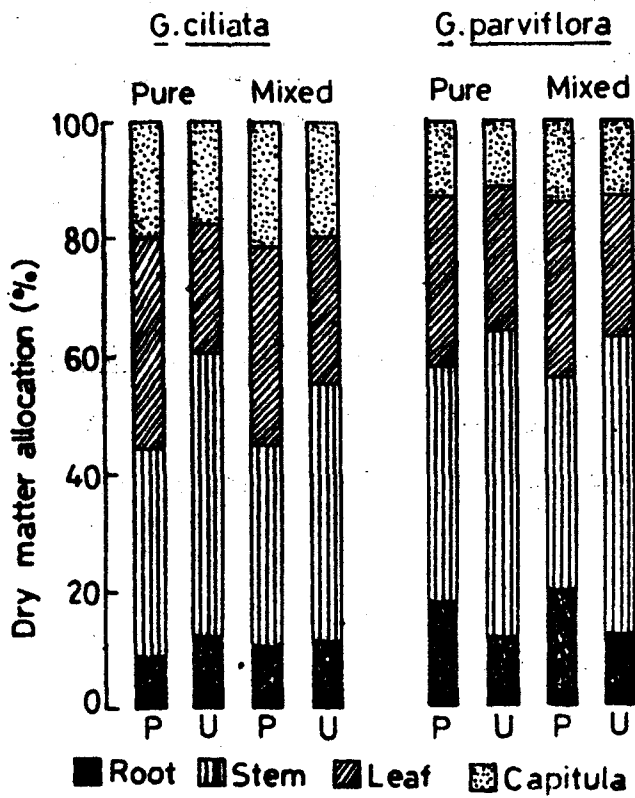


Fig. 7-5

DISCUSSION

A fairly high fraction of the natural populations of both species of Galinsoga was damaged by the herbivores which caused defoliation of plants. The reproductive success of such populations was greatly reduced and mortality increased. Feeding damage by herbivores has also been reported to cause plant mortality in other species (Chatters & Schlehner, 1951; Kulman, 1971; Dixon, 1975; Rausher & Feeny, 1980). Relatively greater mortality risk in the young populations as seen in this study may be due to the fact that the defoliation caused by the herbivores in young stage of growth may render the plants incapable of synthesising enough assimilates required for the production of new leaves for their sustenance. This argument finds support from Janzen (1971). Further, more damage caused by the herbivores to G. parviflora may be attributed to its higher content of triterpenes, saponins, tanins, flavonoids and glucosides which make it more preferable for the phytophagous insects and other herbivores (Plekhanova et al., 1977).

Herbivore feeding caused significant reduction in dry matter production of the two weeds as has been observed by Jameson (1963), Kulman (1971), Bentley & Whittaker (1979) and Whittaker (1982) in other species. Comparatively greater reduction in biomass of G. parviflora may be linked with its preferential feeding by the herbivores, especially in the mixed populations where the defoliation might reduce the competitive ability of G. parviflora, thus forcing it to occupy a subordinate position. In the mixture, the leaf number and leaf area per plant of this weed were also reduced. However, both species

registered an increase in foliage production in response to defoliation showing a strategy to cope with herbivory (Owen & Wiegert, 1976). In contrast to the observation made by Caldwell et al. (1981), the present study depicts that a species which produced greatest foliage surface suffered most from herbivory.

A reduced amount of photosynthetic tissues of G. parviflora in the mixed population, not only caused decrease in its own yield (Fig.7.3) but also conferred competitive advantage on G. ciliata. Less than one (<1) RYT value obtained in the unprotected plots is in conformity with the earlier works (Windle & Franz, 1979). In another study (Chapter VI) it was observed that G. ciliata did not show competitive superiority over G. parviflora in the mixed population even at a density level of 810 plants/m², while in the present study G. ciliata proved to be a stronger competitor than G. parviflora at a lower density (576 plants/m²). This suggests that under the influence of herbivores, G. parviflora may suffer in competition with G. ciliata in moderately dense populations.

A substantially reduced seed output of the two weeds when exposed to predation signifies the role of herbivory in their population regulation. The plants exposed to herbivore feeding have a much lower chance of reaching reproductive phase and of producing seeds, than does a plant protected from herbivory, especially in G. parviflora where predation caused delay in flowering. A similar delay in the onset of reproduction consequent on defoliation has been observed by Collins & Aitken

(1970) in Trifolium subterraneum and by Dirzo & Harper (1980) in Capsella bursa-pastoris. Further, the situation would have been still worse if the seed predation, as reported in other species (Davidson, 1977; Borchert & Jain, 1978; Brown et al., 1979), had also occurred in these weeds.

As has been found for other plant species (Ellison, 1960; Jameson, 1963; Bentley & Whittaker, 1979; Rausher & Feeny, 1980), the reduction in root allocation due to defoliation was observed in G. parviflora but not in G. ciliata. Such a reduction in root allocation may be attributed either to: (i) the transportation of plant resources that are used to produce new leaves after defoliation from the roots or (ii) reduction in the total amount of photosynthate that is transported to the roots for storage due to decrease in growth rate as a consequence of defoliation. However, the data do not help in determining the relative importance of these alternatives in resource allocation to the roots.

The results indicate that herbivory has an important role to play as a bio-regulator of plant populations, although the two weeds attempted to cope with it either by producing more leaves or by maintaining the aboveground biomass at the expense of the roots. Both the species are palatable but slightly more preference was observed for G. parviflora, as a result of which the other component in the mixture i.e. G. ciliata becomes more competitive in the predated plots, while in the absence of herbivory G. parviflora was not

suppressed by G. ciliata. It has been argued (Sibma et al., 1964; Windle & Franz, 1979; Lee & Bazzaz, 1980) that a susceptible or preferred species is affected more severely by herbivore when it occurs simultaneously with interspecific competition. This seems to be largely true with G. parviflora which manages to co-exist with G. ciliata in the herbaceous communities in nature but occupies a subordinate position. Herbivory, thus assumes a great significance as a factor deciding the outcome of competitive interaction among plant species and it may contribute a great deal to the population regulation of certain weedy species like G. parviflora.

CHAPTER VIII

Effect of light intensity and 2,4-D on the Galinsoga
populations

INTRODUCTION

Among the herbicides, 2,4-D has been most widely used for controlling the dicot weeds. Any attempt to control a species through chemical means must take into consideration the effect of the herbicides when applied at different stages of plant life. A few interesting studies have been made by Mc Ilrath & Ergle (1952) and Klingman (1953) on the effect of 2,4-D applied at different growth stages of cotton and wheat plant respectively. Khosla (1969) studied the effect of 2,4-D on growth of seedlings of some weedy species. Although the effect of 2,4-D on weeds has been studied by various workers, the effect of other environmental factors such as light intensity in conjunction with 2,4-D on population regulation of weeds has not been studied intensively.

In the present study an attempt has been made to evaluate the effect of two concentrations of 2,4-D and light intensity both singly and in combination on the population growth of two cohabiting annual weeds, G. ciliata and G. parviflora. As the two weeds exhibit more than one seedling cohorts emerging at different times (Usami, 1976), the populations are likely to be represented by the individuals of different age groups. The experiment was, therefore, extended to study the effect of 2,4-D when applied at different stages of growth of the two weeds.

MATERIALS AND METHODS

The experiment was conducted in an unheated polythene roofed nethouse which was partitioned into two compartments. The roof and two sides (east and west-facing) of one of these compartments was covered with coarse cloth from inside for reducing the solar radiation to 75% of that available in the other compartment which was uncovered. The experimental plants grown in the two compartments were thus exposed to reduced and normal light conditions, henceforth referred to as the low and high light regimes.

Freshly collected seeds of G. ciliata and G. parviflora were separately sown in experimental pots (21 cm diam. with a basal drainage hole) on 5 March 1982 and the each pot was supplied with equal amount of water. After seedling emergence population was thinned down to 20 per pot on 15 March 1982. The aqueous solution of 2,4-D was sprayed in two concentrations on two different stages of plant life. The two herbicide concentrations (low and high) were 3 mg per pot or 0.9 kg per hectare and 6 mg per pot or 1.8 kg per hectare and the two stages of plant growth were seedling and flowering stage. The dates of herbicide application were March 25 and May 4, 1982. On each date of herbicide application 3 pots of either species under each of the two light regimes were sprayed with respective concentrations of 2,4-D. Thus 2 concentrations of 2,4-D x 2 times of application x 2 light regimes x 3 replicates = 24 pots was the experimental plan for each of the two species. Besides

these, 3 extra pots for each of the two light regimes were kept as control where 2,4-D was not sprayed.

The number of survivors and fertile plants per pot and number of capitula and seeds per plant and per unit area were determined in July 1982 after 18 weeks from the start of the experiment when majority of the capitula had matured and completed seeding. After recording the above observations, plants were uprooted whole and leaf area was measured. The biomass was determined by drying the plant material to constant weight in a hot air oven at 80°C for 48 h.

The mature seeds harvested from each pot were kept in labelled polythene bags and were weighed in lots of 50 seeds per sample for estimating the crude reproductive effort (Harper & Ogden, 1970). The seed viability was tested by using 0.1% aqueous solution of tetrazolium chloride (as outlined by Misra, 1968).

Data were statistically analysed and LSD and SE. values were calculated.

RESULTS

Plant survival:

Both species showed greater survival under high light regime where 2,4-D was not sprayed, but in the pots sprayed with 2,4-D G. ciliata showed better survival in low light regime (Fig. 8.1).

Fig. 8.1: Plant survival of G. ciliata and G. parviflora in relation to concentration and time of application of 2,4-D under two light regimes. Explanation of the symbols: circles represent high light regime and triangles low light regime; open symbols for the application of 2,4-D at seedling stage and filled symbols at flowering stage.

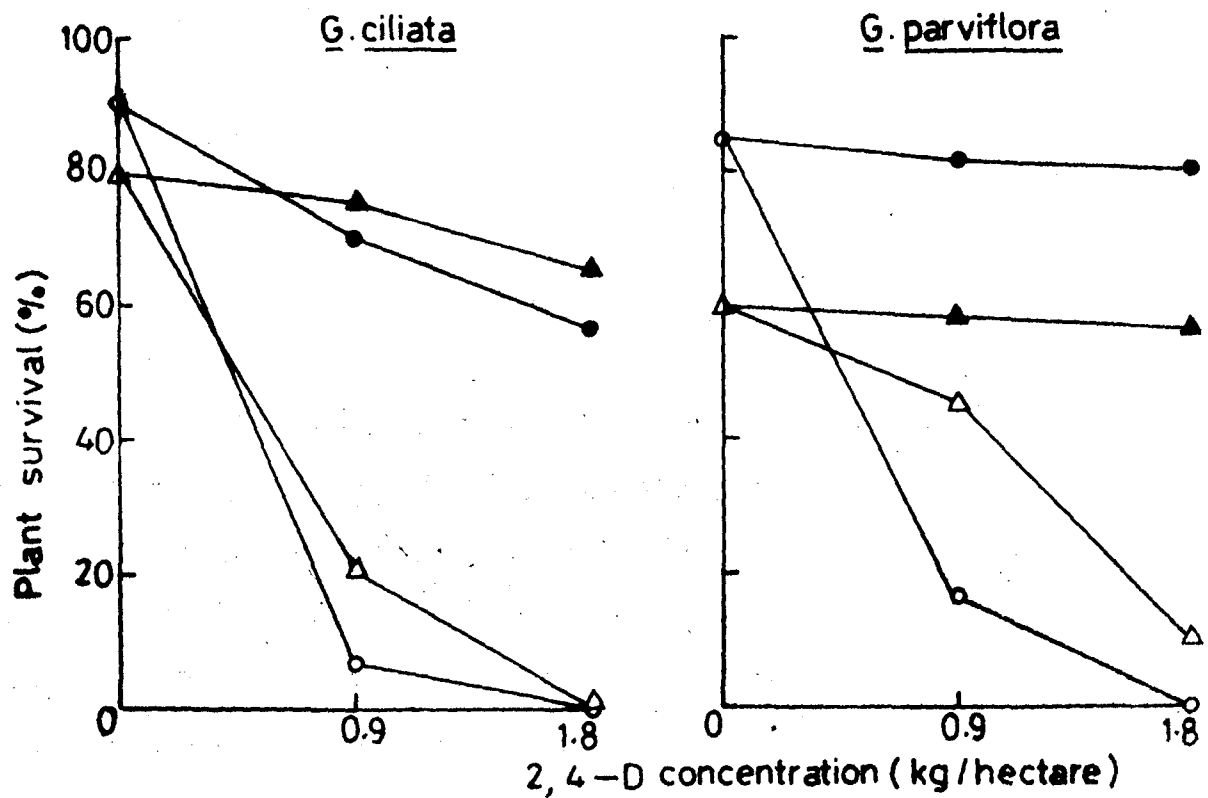


Fig. 8-1

Application of 2,4-D at seedling stage caused relatively greater mortality which increased at the higher concentration. However, mortality of the two weeds in response to 2,4-D was far less under low than at higher light regime. The higher concentration of 2,4-D resulted into death of all the plants of G. parviflora under high light regime while at low light intensity at least 10% of them managed to survive.

Biomass accumulation:

Per plant biomass of the two species decreased due to reduction in light intensity, the effect being more conspicuous in G. parviflora (Table 8.1). The reduction in plant biomass was direct function of 2,4-D concentration. The low concentration of 2,4-D sprayed during flowering caused much more reduction in biomass as compared to that applied in seedling stage, but the higher concentration showed reverse trend. The effect of 2,4-D was more pronounced under high than under low light regime.

Total yield of both species decreased with increased 2,4-D concentration and decreased light intensity, the decrease being more pronounced where 2,4-D was applied at the seedling stage (Fig. 8.2). G. ciliata was less affected than the other species due to change in light intensity, and G. parviflora was comparatively less affected by the 2,4-D treatments. Although 2,4-D application at the flowering stage caused reduction in biomass of the two weeds at low light regime, the effect did not differ due to the herbicide concentration.

Table 8.1: Biomass per plant (mg \pm S.E.) of G. ciliata and G. parviflora as affected by time and concentration of 2,4-D application and light intensity.

Species	Light intensity	Control	Low concentration		High concentration	
			Seedling stage	Flowering stage	Seedling stage	Flowering stage
<u>G. ciliata</u>	High	516.6 \pm 21.4	430.7 \pm 16.6	377.1 \pm 12.8	0.0 \pm 0.0	200.8 \pm 24.6
	Low	313.8 \pm 18.5	250.0 \pm 26.1	234.6 \pm 22.2	0.0 \pm 0.0	146.2 \pm 13.5
<u>G. parviflora</u>	High	645.9 \pm 28.4	572.7 \pm 20.6	557.1 \pm 18.9	0.0 \pm 0.0	320.0 \pm 21.3
	Low	350.8 \pm 16.2	233.3 \pm 14.6	224.4 \pm 17.5	205.0 \pm 9.8	185.8 \pm 16.8

Fig. 8.2: Yield of G. ciliata and G. parviflora as affected by the concentration and time of application of 2,4-D under two light regimes. Explanation of the symbols is the same as in Fig. 8.1.

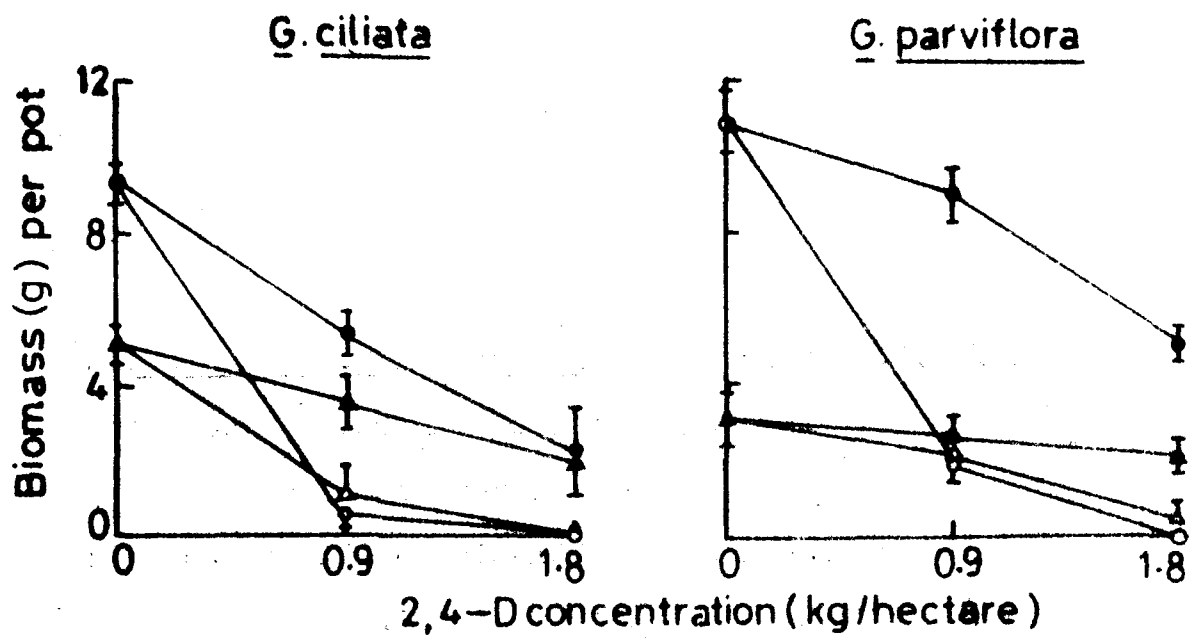


Fig. 8.2

Leaf area ratio:

In both weeds, leaf area ratio decreased at the higher concentration of 2,4-D (Fig. 8.3), but the decrease was more marked in G. ciliata under the high light regime. G. ciliata showed maximum leaf area ratio when grown at low light regime without herbicide application. The reduced light intensity caused increase in leaf area ratio in other treatments as well.

G. parviflora exhibited maximum leaf area ratio where the plants were grown at high light regime and were sprayed with low concentration of 2,4-D at seedling stage. In contrast to G. ciliata, the leaf area ratio of G. parviflora decreased at low light regime (Fig. 8.3).

Seed production:

Seed output per plant and per pot in both the species decreased with increased 2,4-D concentration and reduced light intensity (Table 8.2 & 8.3, Fig. 8.4). In G. ciliata the concentration of 2,4-D reduced per plant seed production by 10-fold compared with 3-fold decrease in G. parviflora. The effect of 2,4-D was much more pronounced on G. ciliata whilst G. parviflora was more affected by light.

At low light regime, the reduction in seed output of G. parviflora due to 2,4-D was insignificant. However, the time and concentration of 2,4-D spraying appear to be quite important. The lower concentration of 2,4-D applied at the seedling stage

Fig. 8.3: Leaf area ratio of G. ciliata and G. parviflora as affected by the concentration and time of application of 2,4-D under two light regimes. Explanation of the symbols is the same as in Fig. 8.1.

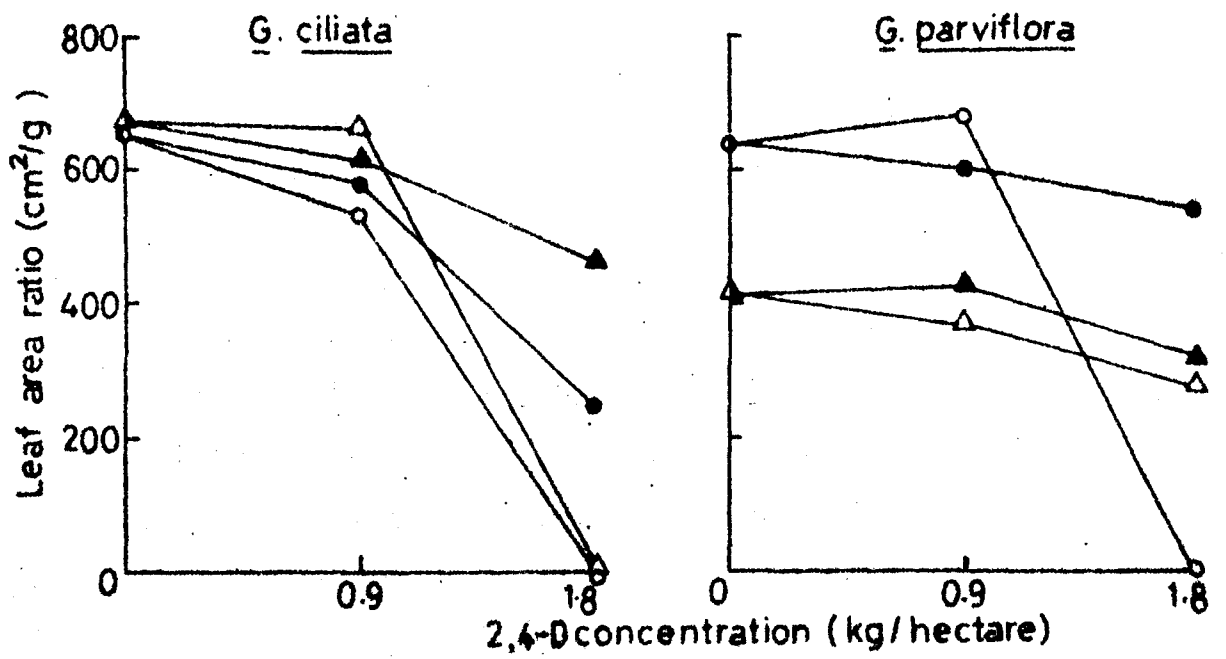


Fig. 8-3

Table 8.2: Average number of capitula/plant, seeds/capitulum and seeds/plant and crude reproductive effort of G. ciliata as affected by 2,4-D application and light intensity (\pm S.E.).

Light intensity	Concentration	Time of application	Capitula/plant	Seeds/capitulum	Seeds/plant	CRE
High	o (control)		16.8 \pm 1.2	18.3 \pm 1.9	308 \pm 32.3	18.9
	Low	Seedling stage	5.0 \pm 0.6	14.3 \pm 1.6	72 \pm 8.9	5.9
		Flowering stage	6.4 \pm 0.4	12.1 \pm 0.8	78 \pm 9.4	4.6
	High	Seedling stage	-	-	-	-
		Flowering stage	4.0 \pm 0.3	9.2 \pm 1.6	37 \pm 5.3	4.2
	Low	o (control)		12.6 \pm 1.0	16.8 \pm 2.1	211 \pm 22.5
Low		Seedling stage	3.0 \pm 0.6	15.7 \pm 1.9	47 \pm 6.1	4.2
		Flowering stage	3.6 \pm 0.4	10.2 \pm 1.4	37 \pm 4.8	3.5
High		Seedling stage	-	-	-	-
		Flowering stage	2.0 \pm 0.3	10.2 \pm 1.3	20 \pm 2.6	3.1

Table 8.3: Average number of capitula/plant, seeds/capitulum and seeds/plant and crude reproductive effort of G. parviflora as affected by 2,4-D application and light intensity (\pm S.E.).

Light intensity	Concentration	Time of application	Capitula/plant	Seeds/capitulum	Seeds/plant	CRE
High	o (control)		12.3 \pm 1.8	26.3 \pm 2.0	323 \pm 36.5	13.4
	Low	Seedling stage	8.6 \pm 0.9	27.5 \pm 2.1	236 \pm 22.8	10.5
		Flowering stage	10.5 \pm 1.2	22.3 \pm 1.9	234 \pm 23.6	9.1
	High	Seedling stage	-	-	-	-
		Flowering stage	4.9 \pm 0.4	20.6 \pm 1.8	101 \pm 15.2	7.8
	Low	o (control)		3.2 \pm 0.4	22.2 \pm 1.9	71 \pm 6.8
Low		Seedling stage	2.9 \pm 0.3	22.8 \pm 2.1	66 \pm 7.5	7.0
		Flowering stage	2.6 \pm 0.3	22.1 \pm 1.3	57 \pm 4.3	6.2
High		Seedling stage	2.0 \pm 0.3	21.2 \pm 1.3	42 \pm 3.4	5.2
		Flowering stage	1.1 \pm 0.2	17.8 \pm 1.2	18 \pm 2.9	3.3

Fig. 8.4: Seed output of G. ciliata and G. parviflora as affected by the concentration and time of application of 2,4-D under two light regimes. The symbols (▣) and (▤) represent 2,4-D application at seedling and flowering stages respectively. Open bars represent the values in control treatment.

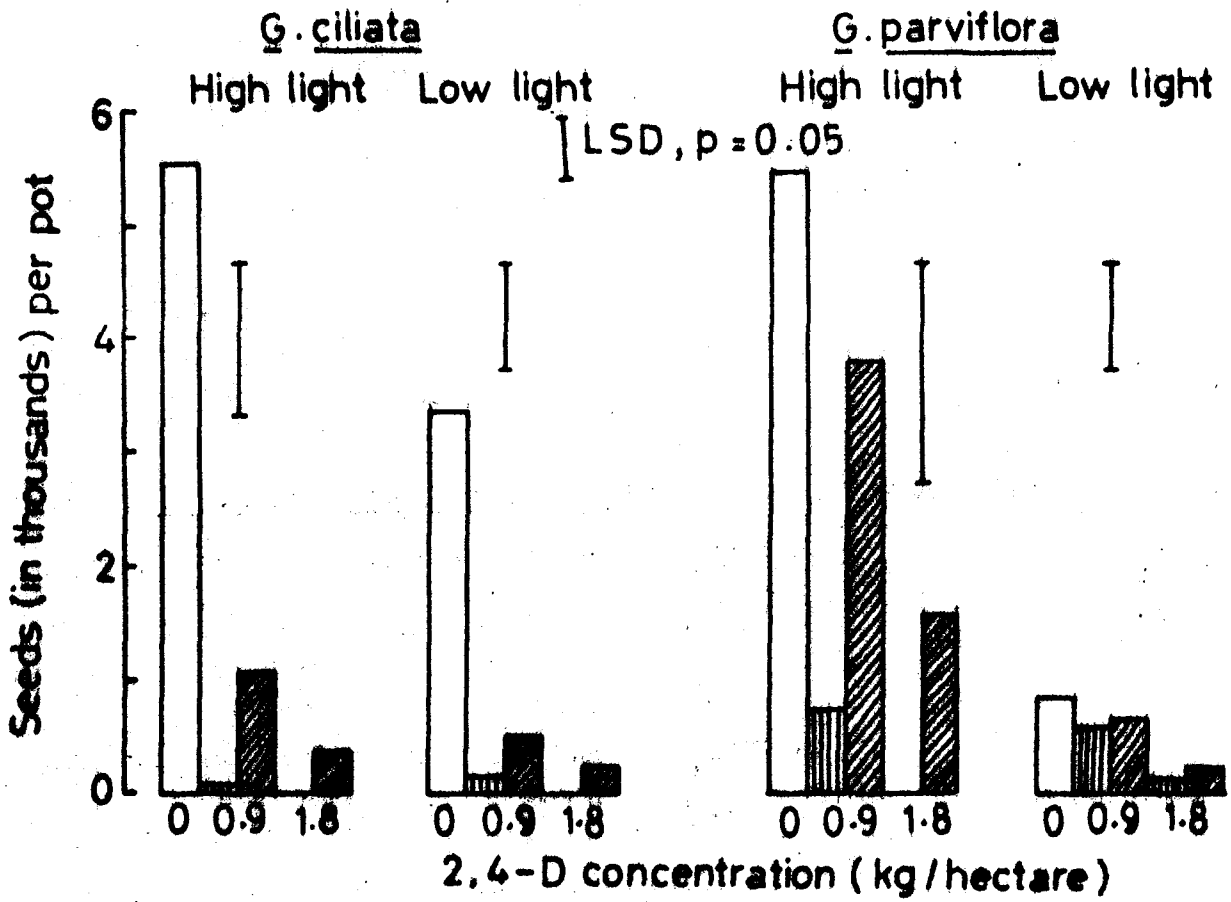


Fig. 8.4

had much more reducing effect on the seed production than even the higher concentration used at the flowering stage. However, differences in seed output per pot was primarily due to differences in number of flowering plants under these treatments.

Crude reproductive effort:

Crude reproductive effort of the two weeds decreased at the higher concentration of 2,4-D and decreased light intensity (Table 8.2 & 8.3). Like other parameters, CRE of G. ciliata was also more affected by 2,4-D than by light, while the other weed was more affected by light. However, the CRE of G. ciliata was greater than G. parviflora.

Seed viability:

Seeds collected from the plants grown under the high light regime showed greater viability in comparison to those produced under the reduced light intensity (Table 8.4). The use of 2,4-D at the flowering stage caused greater loss of seed viability as compared to 2,4-D spray at the seedling stage. The viability was further reduced with increasing concentration of 2,4-D.

DISCUSSION

The results suggest that the two weeds experienced greater mortality due to herbicide application and reduction in light intensity. Increased mortality due to increase in 2,4-D concentration as observed in the present study has also been

Table 8.4: Seed viability (%) of G. ciliata and G. parviflora as affected by time and concentration of 2,4-D application and light intensity.

Species	Light intensity	Low concentration		High concentration		
		Control	Seedling stage	Flowering stage	Seedling stage	Flowering stage
<u>G. ciliata</u>	High	94	100	42	-	26
	Low	89	86	56	-	40
<u>G. parviflora</u>	High	100	100	60	-	42
	Low	64	78	61	62	34

reported by other workers (Das & Laloo, 1978). Such a response may be attributed to the increased concentration of 2,4-D in plant body, which reduces the uptake of minerals from the soil (Cooke, 1957) and rate of photosynthesis (Loustalot & Muzik, 1953). The unfavourable effect of 2,4-D on these two physiological processes might cause plant mortality and the seedling populations being most susceptible suffered the heaviest mortality. Relatively greater mortality in G. parviflora at reduced light regime highlights the importance of light in regulating the population of this weed.

A substantial reduction in yield of the two species in response to the herbicide spray is in agreement with the observations made by Mc Ilrath & Ergle (1952), Klingman (1953) and Bhan et al. (1970) on other plant species. Mc Ilrath & Ergle (1952) also reported the maximum effect on seedlings, which supports the observations of the present study. Comparatively greater reduction in per plant biomass of G. ciliata due to herbicide may be attributed to its hairyness which might facilitate the absorption of 2,4-D as argued by Klingman (1973). The mild effect of 2,4-D under reduced light condition may be linked with poor absorption of the herbicide under such conditions (Blackman & Robert-Cunninghame, 1955; King, 1974).

The two weeds responded differently to light intensity. At low light regime the leaf area ratio of G. ciliata increased substantially, while in G. parviflora a sharp decrease was observed. This suggests that G. ciliata may grow successfully

in the areas receiving low light intensity, whereas G. parviflora shows poor growth on such habitats. It has been suggested (Pandey & Sinha, 1977) that the species adapted to low light intensity show increase in leaf area ratio with reduction in light intensity. Thus, G. ciliata may be considered as a relatively shade-tolerant species.

Although both species showed plastic-reduction in seed output as a result of decreased light, the reduction was much greater in G. parviflora, indicating that both the species tend to respond similarly to light conditions, but during the course of evolution they might have become adapted to different light intensities.

The decrease in seed viability of the two weeds in response to herbicide application is in agreement with the observations of Taylorson (1966), Powell & Taylorson (1967) and Maun & Cavers (1969) on other plant species. Crude reproductive effort of the two weeds also decreased due to the herbicide application and reduction in light. However, the two different concentrations of 2,4-D used at seedling stage had almost the same effect. Maun & Cavers (1969) and Dubey & Mall (1975) have also observed that different concentrations of the herbicide used either as pre-emergence treatment or at the seedling stage of plant do not exhibit differential effect in long run.

It may be concluded that the application of 2,4-D at seedling stage provides an effective control measure for the

two weeds which not only showed heavy mortality but also exhibited substantial plastic reduction in reproductive growth. Further, the study reveals that the efficacy of 2,4-D was modified by the light intensity and age of the weeds at which it was applied. Thus the population of these two weeds may be effectively regulated by the herbicide only when the environmental factors (light in the present case) are favourable for herbicide action and the application is made at the vulnerable stage of plant development.

General Discussion

GENERAL DISCUSSION

The data on the dynamics and regulation of populations of the two species of Galinsoga presented in the preceding chapters, reveal the possible role of environmental factors operating at different growth phases to regulate their population size. Both the weeds have a fairly high population of seeds in soil, of which a very small fraction could give rise to mature plants. This indicates that at each stage of life cycle there may be successive ~~elimination~~ elimination of individuals from the population either through mortality or through non-functioning.

Seed germination studies in relation to seed sowing density of the two species (Chapter V) indicate that increased seed input **does not** always ensure the proportional increase in seedling population. Such reduction in seed germination provides regulatory mechanism to population as has also been argued by Palmblad (1968a). Harper (1961) and Yadav & Tripathi (1981) opined that seed germination and establishment of a plant species is determined by the interaction of soil seed bank and available 'safe microsites'. In cropland situation, in spite of high seed population in soil, both weeds showed poor seed germination in 1981 (Chapter III) which may be due to increased density of associates. This is also confirmed by the results where the seeds introduced to established vegetation showed poor germination (Chapter IV). The decrease in seed germination of the two species due to associates may be

attributed to lack of enough 'safe-sites' (Harper & Gajic, 1961; Tripathi & Dwivedi, 1978) and/or production of some seed germination inhibitors by the associated vegetation. Eupatorium riparium and E. adenophorum which grow as the dominant associated species on the study plots are known to have allelopathic effect on seed germination of the two weeds (Tripathi et al., 1981; Rai & Tripathi, 1982b). Further, the sowing of seeds of the Galinsoga species in clumps gave better germination, which might be accounted by the production of promotary chemicals and/or the combined force of simultaneously growing several radicles that may help them in emergence as suggested by Linhart (1976). Besides, the abiotic factors such as moisture stress, soil texture (Chapter V), low temperature during winter and reduced light have been observed to exercise considerable influence on the seed germination and growth of the two weeds.

After emergence, seedlings have to face various environmental hazards together with competition for resources, which reduce their establishment and growth as shown by density-dependent mortality in the two weeds (Chapter V & VI). The high juvenile mortality caused by the environmental constraints has also been reported in other species by earlier workers (e.g. Williams, 1970; Hett, 1971; Sarukhan & Harper, 1973; Bazzaz & Harper, 1976; Yadav & Tripathi, 1981; Silvertown & Dickie, 1981). Pelton (1962) has identified various factors causing seedling mortality. In the present study vegetation

cover, predators, moisture stress and reduced light appear to be the major factors contributing to heavy seedling mortality. The role of vegetation cover in seedling mortality is clearly established by the greater survivorship of G. ciliata and G. parviflora in cleared plots (Chapter IV). The release of allelochemicals from E. riparium (Chapter IV), application of 2,4-D (Chapter VIII) and predation by the slugs (Chapter VII) also affected the seedling survival of the two species. These observations indicate the role of these factors in population regulation of the Galinsoga species.

The mortality of individuals continues even after the establishment of seedlings as indicated by Deevy's Type II and III survivorship curves. The mortality beyond seedling stage may be largely due to severe competition offered by the growing vegetation and low temperature in winter season. In experimental condition too, both weeds exhibited severe mortality at low moisture regime which was exaggerated at high population density (Chapter V). The suppressive effect of associates was so much that none of the seedlings of G. parviflora survived over a 5-months study period. The increasing density of associates caused 20% reduction in light intensity which in turn might have resulted into severe mortality in the two weeds in cropland situation. The large effect of light is also confirmed by the severe plant mortality (especially in G. parviflora) observed under the reduced light (Chapter VIII). This is in agreement with observations of Tamm (1956) and Singh (1980) indicating poor establishment and survival in certain

other plant species grown/introduced into established communities.

The seedling cohorts of Galinsoga species emerging earlier showed greater survivorship and longer half-life than the late emerging ones (Chapter III) as has been observed by Sarukhan & Harper (1973), Hawthorn & Cavers (1976), Weaver & Cavers (1979) and Weiss (1981) in other plant species. A similar observation was made in experimental condition too (Chapter IV). The cohorts of G. ciliata, however, exercised more adverse effect on later arriving cohorts, as compared to that of G. parviflora which indicates the relative importance of these weeds in regulating their own populations. Seedlings of G. parviflora experienced maximum mortality when grown with 25 days old cohort of G. ciliata which was even larger than that observed with 50 days old cohort. This implies the age-dependent fluctuation in degree of interference which explains the greater survivorship of III cohort of G. parviflora relative to that of II cohort in the permanent quadrats (Chapter III). However, an experiment in which both species were grown in mixture at varied density and soil nitrogen levels reveals that at lower density the suppressive effect of G. ciliata on G. parviflora was not marked but as the density increased the former species caused mortality in the population of latter. This highlights the importance of G. ciliata in population regulation of the other species in nature where the two weeds often grow together in dense populations.

Sharitz & Mc Cormick (1973) suggested that the biotic factors regulate the population of Sedum smallii and Minuartia uniflora largely through thinning of individuals whereas the abiotic factors through stunting of individuals. However, in the present study it was observed that the populations of both species of Galinsoga are regulated through heavy mortality caused by both biotic and climatic influences. The seedlings that manage to survive the unfavourable conditions, responded to biotic and abiotic factors mainly through plasticity in rest of their lives.

Density had a negative effect on growth of G. ciliata and G. parviflora. The reduced seed output/input ratio in crowded populations (Chapter V) indicates the self-regulation of populations of the two weeds. Further, the decrease in per plant yield and seed output of the two weeds due to crowding, as has also been observed by other workers in several other species (e.g. Yoda et al., 1963; White & Harper, 1970; Myerscough & Marshall, 1973; Tripathi & Gupta, 1980; Tripathi & Yadav, 1982), indicates the role of density in their population regulation. A comparison of responses of the two weeds to increasing density reveals that G. parviflora is more susceptible to crowding as it showed relatively greater skewness in frequency distribution of biomass and capitula number as compared to the other species (Chapter VI). A plastic reduction in crude reproductive effort (CRE) of G. parviflora due to density increase also supports its greater susceptibility to crowding. Conversely, the CRE of G. ciliata increased with

density, suggesting that with increase in severity of competition it devotes more resources to reproduction, a response exhibited by other species under stressed condition (Gadgil & Solbrig, 1972; Hickman, 1975).

The available soil moisture plays an important role in population regulation of the two species which reduced the seed output and biomass production so much that the interacting effect of density became negligible. However, the two weeds showed better growth and seed output in sandy loam soil at high moisture regime (Chapter V), thus indicating the role of soil texture and moisture in population regulation. Trivedi & Tripathi (1982b) have also observed better growth of Spergula arvensis in sandy soil at high moisture regime. The study pertaining to interacting effect of soil nitrogen and population density on seed production of the two weeds reveals that at low nitrogen level seed output of the two weeds declined at high population density, while at high nitrogen level G. ciliata showed constant increase in seed output with density (Chapter VI) indicating that on nitrogen rich habitats increase in population density does not restrict the seed production by G. ciliata.

Seed germination and seedling growth of both weeds was retarded when either treated with aqueous extracts of E. riparium or grown in soil amended with plant residue of E. riparium (Chapter IV). The poor growth of radicle and plumule caused due to inhibitory action of E. riparium might

render the Galinsoga species weak enough to compete against E. riparium, and as such, the competitive and allelopathic effects of E. riparium would be a key factor in regulation of Galinsoga population. In natural populations the feeble growth and increased death of seedlings of the two species of Galinsoga introduced or emerged in close vicinity of E. riparium may be partly attributed to the allelopathic effects of E. riparium. It is likely that some other plant species might also be involved in regulating the populations of Galinsoga species through chemical means, but this remains to be investigated. However, there is enough evidence to show that allelopathy is an important factor in population regulation (Friedman et al., 1977; Parker & Muller, 1979; Rai & Tripathi, 1982b). Putnam & Duke (1974) and Lockerman & Putnam (1979) have clearly demonstrated the role of allelopathic effects of cucumber (Cucumis sativus L.) in biological suppression of white mustard and weed populations.

The herbivore predation on natural populations of the Galinsoga species caused seedling mortality and reduced the yield and seed output significantly, thus indicating the role of predation in the population regulation. Whittaker (1982) has reported a similar decrease in biomass production and plant survival of Rumex crispus in response to grazing by chrysomelid beetle. The results indicate that G. parviflora suffers more due to herbivory than G. ciliata. The preferential feeding of G. parviflora in mixed population not only caused decrease in its own yield but it also provided a competitive advantage

to co-existing G. ciliata. This is confirmed by less than one RYT value ($RYT < 1$) in the unprotected plot compared to RYT greater than one ($RYT > 1$) in protected plot. G. ciliata is, of course, a better competitor as revealed by the data in Chapter VI, the herbivory confers further competitive superiority on G. ciliata over G. parviflora in natural populations, where the former species was more dominant even in moderately dense population. The visual observation of Babu (1977) on the relative abundance of the two species in nature is confirmed by the present study.

The study pertaining to interacting effect of light and 2,4-D concentrations (Chapter VIII) showed that although G. ciliata is greatly susceptible to 2,4-D, and G. parviflora to light, both the species exhibited poor growth when grown in bright light conditions and sprayed with high concentration of 2,4-D at seedling stage. This suggests that effective control of these two species of Galinsoga by 2,4-D is possible only when an appropriate concentration of 2,4-D is sprayed at early stage of plant life on sunny days. The application of 2,4-D at flowering stage of ~~these~~ weeds is also significantly important as it caused greater loss of seed viability as compared to the herbicide application at seedling stage. Any factor, force or treatment that adversely affects reproductive parameters becomes important in so far as the population growth in successive generations is concerned.

The responses with reference to vegetative growth exhibited by these weeds to light seems to be quite adjusted to their natural habitats, G. parviflora a weed of cropland and disturbed wasteland occurring in nature as subordinate of

co-existing G. ciliata which showed luxuriant infestation. Besides other factors, a substantial decrease in leaf area ratio of G. parviflora due to decrease in light intensity explains its feeble growth and greater susceptibility to associates in the cropland due to increased plant density during second year of study (Chapter III).

Although both species of Galinsoga produce enormous seeds every year, their natural populations do not seem to show proportional increase in size, indicating that various abiotic and biotic factors of environment operate at different growth phases to regulate their population size. The two weeds responded to these factors both through mortality and plasticity. G. ciliata showed lesser mortality and also absorbs greater density and light stress as compared to G. parviflora (Chapter V, VI & VIII), while the later, besides showing greater mortality and susceptibility to crowding and light was also preferred more by the herbivores (Chapter VII). Thus, G. parviflora population being more susceptible to herbivory and light stress and density increase is less successful than G. ciliata as indicated in the foregoing paragraphs. However, the competitive superiority of G. ciliata over G. parviflora does not effect G. parviflora so adversely as to cause elimination from the mixed populations. Obviously, the interacting influence of several other factors (including competitive effect of other associated plant species on G. ciliata) must be regulating the populations of the Galinsoga spp. in a complex manner:

The two weeds being the members of plant communities growing on highly disturbed wasteland and cropland habitats appear to have developed a strategy to cope with the prevailing frequent disturbances (e.g. road construction in wasteland and weeding and herbicide and fertilizer application in cropland), by producing as many as three seedling cohorts in a single year, all of which are capable of completing the life cycles successfully within a short period if the conditions are favourable. The existence of the three cohorts appearing at different times of the year also ensures the successful perpetuation of the Galinsoga spp. in the event of unfavourable conditions prevailing over a part of the year. In absence of biotic disturbances, as was the case in the permanent quadrats, both weeds exhibited poor growth indicating that the populations of the two weeds are also characterised by the properties of self regulating systems imposing restrictions on the population growth beyond an optimum level.

(Although sufficient information on various aspects of population regulation of G. ciliata and G. parviflora has been provided by the present study, it is felt that studies pertaining to population behaviour of the biotypes, of the two weeds, if any, in relation to climatic, edaphic and biotic factors, adaptive significance of seed polymorphism in population dynamics and a detailed study on the dynamics of the seed population in soil and identification of the factors affecting the soil seed bank might provide more clues with respect to the population regulation of these two weeds.)

Summary

The present investigation deals with the dynamics and regulation of population of the two common annual weeds (Galinsoga ciliata (Raf.) Blake and G. parviflora Cav.) of Meghalaya. An attempt has been made to identify some of the major factors which contribute to regulation of their population. Both species of Galinsoga are exotic, short-lived herbs of family Asteraceae and grow luxuriantly at higher altitudes (from 950 to 1750 m) in the hilly areas of the North-Eastern region. Besides being the weed of disturbed wastelands, they also infest the cropfields and kitchen gardens causing reduction in productivity of hill agro-ecosystems.) (Apart from their abundance and economic importance, the two species of Galinsoga are also quite interesting from ecological view point. They represent sympatric, closely related pair of species with synchronous life cycle which is completed within two months. Thus, a study on the population dynamics of the two Galinsoga spp. were carried out from April 1980 to December 1981 in field situations, and (the effect of various factors such as associated vegetation, their own adult plants, predation, seed sowing density and pattern, population density and soil texture, soil moisture, soil nitrogen and light intensity and 2,4-D application on the population behaviour of these weeds was studied. A brief summary of the results on the various aspects is given below:

- 1) Population dynamics of the seedling cohorts as influenced by site conditions and date of emergence:

Seedling emergence, survival and reproduction of the two

Galinsoga spp. were studied in permanent quadrats on cropland and wasteland sites by following the fate of individuals at short and regular intervals. Both the weeds are characterized by the presence of the three seedling cohorts emerging in April, May and August in 1980, and March, April and July, 1981. The seedling cohorts exhibited Deevy's Type II and III survivorship curves which were further influenced by site conditions and by date of emergence. In 1980, the seedling emergence, survivorship and seed output of the two weeds were greater on the cropland site than on wasteland, but in the following year a reverse trend was observed. Generally, the late emerging cohorts were less successful than the earlier emerging ones. The increased density of the associates in the cropland situation during second year of study caused 75% reduction in seed output per plant of G. parviflora while the other weed did not show such plasticity.

ii) Effect of associated vegetation and their established cohorts:

(a) The effect of associated vegetation was evaluated by introducing the seeds and transplants of the two species in vegetation-cleared plots and uncleared plots. The results obtained suggest that the associated vegetation causes spectacular reduction in seed germination and survivorship and growth of the seedlings of the two weeds, the effect being more on the seedlings than on the transplants. Some of the seedlings of G. ciliata could manage to survive over 5 month study period, while the growth of the other species was reduced so much that

the survivorship of its seedlings was nil which indicates the differential susceptibility of the two weeds to resource competition.

(b) Allelopathic effect of Eupatorium riparium : Allelopathic effect of Eupatorium riparium Regel, a dominant ruderal weed at higher altitudes of Meghalaya was also studied on the population of the two Galinsoga species. Seed germination and further growth of seedlings of Galinsoga spp. were suppressed by the aqueous extract and leachate of E. riparium. The suppressive effect was often correlated with the concentration of the extract and leachate. The seed germination and vegetative and reproductive growth of the two weeds also declined considerably in the experimental pots which were filled with the soil either collected from the close vicinity of E. riparium stands or amended with the plant residue of E. riparium.

(c) Effect of established cohorts of the Galinsoga spp.: In pot culture experiment, the late arriving cohorts of both weeds exhibited poor seed germination, survivorship and growth on account of competition from their established cohorts. The suppressive effect of the established cohorts was a direct function of their age. However, the established cohort of G. ciliata exercised greater suppression than the other species. 25 days old cohort of G. ciliata caused maximum suppression in growth of the late emerging individuals of G. parviflora. There was considerable reduction in biomass, number of capitula and seed output of the young cohorts when grown in close proximity of their established cohorts.

iii) Effect of sowing density, sowing pattern and soil moisture and texture:

The population response of the two Galinsoga spp. was studied in relation to sowing pattern (clump or scattered pattern), sowing density and soil moisture and texture. In a given sowing pattern, seed germination of both species declined with increase in sowing density and moisture stress. However, sowing ~~of seeds~~ in clumps and an increased proportion of sand in soil enhanced the germination. The weed population raised from scattered pattern of sowing experienced less mortality than those in clumped distribution. Plants grown at high moisture level matured earlier, and fertility of the survivors was negatively correlated with both density and moisture stress in both species although G. ciliata was less affected.

Seed output and dry matter yield per pot of both species increased with population density but the increase was not linearly related to the increase in plant numbers. However, density-induced reduction in seed output was observed at high densities. G. ciliata appears to tolerate greater density-stress than G. parviflora. A substantial decrease in production of capitula, seeds and dry matter at low moisture level indicates the role played by soil moisture in regulating the population growth of the two weeds. An increased proportion of sand in soil resulted into significantly greater seed production in G. parviflora. G. ciliata also showed a similar trend although the differences were not statistically significant.

iv) Effect of density and soil nitrogen on pure and mixed populations of the two weeds:

The effect of density and soil nitrogen on population regulation of Galinsoga spp. was studied in their pure and mixed stands. Unlike lower densities, at high densities both weeds exhibited some mortality which tended to increase with increase in soil nitrogen. G. ciliata exhibited better survival in mixture than in pure, while G. parviflora showed the reverse trend. The dry matter yield and seed output under the various treatments revealed that G. ciliata is less sensitive to density increase than G. parviflora. With increase in population density both weeds showed increased skewness in per plant biomass and capitula production, but in nitrogen-rich habitats the density effect was relatively mild. At lower densities, both weeds grew better and produced more seeds in mixture than in pure, but at high densities G. ciliata became dominant over G. parviflora. The crude reproductive effort was, however, not appreciably modified due to soil nitrogen and stand nature. The reproductive allocation in G. ciliata increased with density increase while in the other species, a drastic reduction in reproductive allocation was evident at high densities.

v) Effect of herbivory on competitive interaction and growth of the two weeds:

Effect of natural populations of the slug (Marisa dussumieri Gray) and other herbivores was studied on the pure and mixed populations of Galinsoga spp. in field conditions. Predation

caused heavy mortality, especially in G. parviflora. Except in G. parviflora grown in the mixed population, the two weeds produced greater number of leaves under predation pressure but the leaf area decreased drastically. G. parviflora was, however, more susceptible and the flowering and fruiting in this species was also delayed due to herbivory. Predation caused substantial reduction in seed and dry matter production of both the weeds, but the effect was more in G. parviflora. In both weeds the resource allocation to leaves was reduced due to herbivory but the root allocation was reduced only in G. parviflora. The preferential feeding of G. parviflora reduced its competitive fitness in the mixed population.

vi) Effect of light intensity and 2,4-D:

The population response of the two species of Galinsoga was also studied in relation to light intensity and application of 2,4-D. Although plant survival and growth of the two weeds were adversely affected by reduction in light intensity and increased concentration of 2,4-D, G. ciliata was more susceptible to 2,4-D and G. parviflora to light. G. ciliata exhibited increase in leaf area ratio under reduced light regime while G. parviflora showed drastic reduction. The effect of 2,4-D was direct function of its concentration, which was modified by the light intensity and age of plant at which the herbicide was applied. The application of 2,4-D at seedling stage under high light regime caused heavy plant mortality and growth reduction in both the weeds, while the application of 2,4-D at flowering stage caused severe seed mortality.

The study reveals that various abiotic and biotic factors of environment as mentioned above, influence the two Galinsoga spp. at different growth phases and the complex interaction of these factors regulate the growth and maintenance of their populations. Although the two weeds respond to these factors both through mortality and plasticity, G. ciliata is less susceptible. This might confer an advantage on it in competition with G. parviflora in mixed populations in nature. Further, the two species being members of the plant communities of highly disturbed habitats like wasteland and cropland, appear to have adapted to the prevailing habitat conditions by producing enormous seeds every year which ensure their continued survival. Besides, the production of as many as three seedling cohorts in a single year by both the weeds may be viewed as another strategy to offset the risk they have to face in a habitat that is highly disturbed and where they face constant threat of removal by weeding and other agricultural practices.

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